METAPOPULATIONS OF MARSH RABBITS: A POPULATION VIABILITY ANALYSIS OF THE LOWER KEYS MARSH RABBIT (SYLVILAGUS PALUSTRIS HEFNERI)

By

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Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

METAPOPULATIONS OF MARSH RABBITS: A POPULATION VIABILITY ANALYSIS OF THE LOWER KEYS MARSH RABBIT (SYLVILAGUS PALUSTRIS HEFNERI)

By

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The Lower Keys marsh rabbit (Sylvilagus palustris hefneri) is a state and federally endangered subspecies that historically ranged from Big Pine Key to the southernmost of the Florida Keys, Key West. Lower Keys marsh rabbits inhabit the marsh transition zone, an area that is currently highly fragmented due to development. This dissertation incorporates data collected during a 2.5-year study of the population biology, habitat requirements, and spatial structure of the populations of the Lower Keys marsh rabbit.

Within and between patch dynamics were studied by live-trapping marsh rabbits and fitting them with radio-collars at 6 habitat patches. Genetic

variability, growth and morphology, natality, mortality, home range size, and dispersal were estimated from this portion of the research. To study metapopulation dynamics, all patches of marsh rabbit habitat in the Keys were located and sampled with fecal-pellet grids during the 2.5 years to determine presence/absence and density of marsh rabbits at each patch.

Fifty-three marsh rabbits were live-trapped during the study and 43 of were fitted with radio-collars. Compared to other species of rabbits, the Lower Keys marsh rabbits were found to have average genetic variation, lower natality, and higher mortality. Subadult males were the primary dispersers; all but one male left its natal patch at the onset of sexual maturity and moved 180 - 2050 m. Due to the amount of movement between habitat patches, the marsh rabbits appear to exist in a metapopulation.

Fifty-nine patches of transition-zone habitat were located throughout the Lower Keys. Twenty of these patches had pellets present during all of the surveys, 22 had pellets present during at least one of the surveys, and 17 never had any pellets present. Habitat patches that were close to other patches and that had dense vegetation were most likely to be inhabited. When all 59 habitat patches and the information about the population biology of S. p. hefneri were combined in a population viability model, the model predicted that the rabbit would go extinct in the next 20-30 years. Reducing mortality in each life stage had the greatest effect on overall metapopulation persistence.

CHAPTER 1
INTRODUCTION

The primary objective of this dissertation is to develop a population viability analysis (PVA) for the endangered Lower Keys marsh rabbit (Sylvilagus palustris hefneri). The Lower Keys marsh rabbit was first described as a distinct subspecies by Lazell (1984). Lower Keys marsh rabbits have a shorter molariform tooth row, a higher and more convex frontonasal profile, a broader cranium, and a longer dentary symphysis than mainland and Upper Keys rabbits.

Historically, the range of the Lower Keys marsh rabbit extended from Big Pine Key to the southernmost of the Florida Keys, Key West (dePourtales 1877). During the 1970s and 1980s, a decline in Lower Keys marsh rabbits was reported (J. Lazell, pers. comm.) and a study of the rabbit's status was commissioned by the Florida Game and Fresh Water Fish Commission (Howe 1988). Howe (1988) recorded marsh rabbits present at 13 of J. Lazell's (unpubl. data) original 17 sites and absent from 4 of the sites. The Lower Keys marsh rabbit was listed as endangered by the Florida Fresh Water Fish Commission in 1989 (F.A.C. 39-27) and by the U.S. Fish and Wildlife Service in 1990 (U.S. Fish and Wildlife Service 1990).

Three subspecies of marsh rabbits are recognized, S. p. paludicola, S. p. palustris (Chapman and Willner 1981), and S. p. hefneri (Figure 1.1). The marsh rabbit is found in lowlands from the Dismal Swamp of Virginia into the Florida Keys. Little is known about the biology of the Lower Keys marsh rabbit (Chapman and Flux 1990, Wolfe 1992). Compared to other species of cottontails, the biology and ecology of marsh rabbits in general (Sylvilagus palustris spp.) is poorly understood (Chapman et al. 1982).

Tomkins (1935) and Carr (1939) commented on marsh rabbit (S. p. paludicola) behavior in North Carolina and north-central Florida marshes. Blair (1935, 1936) studied the diet and habits of marsh rabbits near Gainesville, Florida. The reproduction of the marsh rabbit (S. p. palustris) was studied by Holler and Conaway (1979) in Belle Glade, Florida.

Despite these studies, large gaps in the knowledge of the population ecology, habitat use, and risk of extinction for S. p. hefneri remain. Extrapolation from these studies to the Lower Keys marsh rabbit may not be accurate. The Lower Keys marsh rabbit inhabits a unique island ecosystem and is subject to different pressures and resources.

Population Viability Analysis

Population viability analysis (PVA) is a comprehensive examination of the interacting factors that put a population (or species) at risk of extinction

(Gilpin and Soulé 1986). In small populations, both stochastic and deterministic phenomena can affect the persistence time of a population. Perturbations that are stochastic include variation in the environment (climatic variation, natural catastrophes), genetic composition (loss of genetic variability, inbreeding depression), or the demographic composition (sex, age ratios) of a population (Shaffer 1981). Demographic and genetic stochasticity are most important in small populations. Environmental stochasticity is important for all populations, and its importance decreases only slightly with increasing population size.

Deterministic causes of extinction include habitat destruction, invasion by introduced predators, disease, and climatic change (Nunney and Campbell 1993). Deterministic extinction can occur regardless of population size, if all of the population is affected. Both stochastic and deterministic phenomena may interact via feed back loops leading to potential extinction via "extinction vortices" (Gilpin and Soulé 1986), and differ in magnitude and importance for species with different life-history attributes. Because knowledge about intrinsic population dynamics of a species is often limited and the occurrence and impact of extrinsic factors is uncertain, PVA can only make probabilistic predictions about a species' future (Ginzburg et al. 1982, Shaffer 1990).

Spatial Structure

Most endangered species live in habitats that have become fragmented (checkerspot butterfly: Murphy et al. 1990; forest-dwelling raptors: Thiollay and Meyburg 1988, spotted owl: see Lamberson et al. 1994). For these species, the spatial structure of the habitat patches may have large effects on the species' persistence. A PVA for a species existing in a fragmented habitat must look at several spatial and temporal scales of resolution (Gaines et al. 1992, Lacy 1993).

Populations occurring in habitat patches may be locally subject to higher risks of extinction than in continuous habitat due to factors (nest predation, increased exotics, microclimate changes) that occur more frequently in smaller areas that have high perimeter-to-area ratios (Lovejoy et al. 1986, Loiselle and Hoppes 1983). These "edge effects" may be intensified in smaller habitat patches, where nearly all of the patch is edge and little is interior (Wilcox and Murphy 1985). Small patches will support fewer individuals, increasing the rate of extinction caused by stochastic events (Gilpin and Soulé 1986).

For populations of species with poor dispersal ability relative to the distance between patches, the time to extinction will be equal to the time that the last local population goes extinct (Hanski and Gilpin 1991). Each patch of habitat represents a population of these species; surviving populations may be said to be relictual (Berry 1986). Harrison (1991, 1994) uses the term "non-

equilibrium" to describe metapopulations where movements between patches are not great enough to increase persistence time. This population configuration has been seen in species isolated by climatic change (Brown 1971), clear-cutting of forests (Leck 1979, Laurence 1982), and man-created islands (Willis 1974, Karr 1982). These relictual species may lack the locomotive ability, evolutionary history, and/or behavioral plasticity to allow them to move between patches, or the configuration of patches may prohibit movement. Some species may exhibit "conspecific attraction" and preferentially colonize patches where conspecifics are present (Smith and Peacock 1990, Ray et al. 1991). These species may be less likely to (re)colonize empty habitat patches than other species.

If individuals of the species are exceptionally mobile, relative to the distance between habitat patches, then the individuals within the patches may frequently interact and form one large demographic entity inhabiting a patchy environment (Harrison 1991). Many highly mobile species of birds (Blake and Karr 1987, Rolstad 1991) use forest patches, wetlands, continental shelf, and oceanic islands in this manner. Other species that are adapted to highly variable environments such as disturbance or "r-selected" species also inhabit temporally and spatially variable habitats but remain a single population (Edwards et al. 1981, Adler and Wilson 1987).

Between these 2 extremes are species that spend at least a portion of their life in 1 habitat patch but are capable of moving to other habitat patches during their lifetime. For populations of these species, local extinctions may be counteracted by colonizations from nearby patches, and the overall persistence time of the species may be collectively longer than the persistence time of any one patch (Levins 1969). Populations of species that exhibit this dynamic are said to exist together as a metapopulation (Levins 1970).

Metapopulations

Recently the term "true or classic metapopulation" has been used to distinguish between this type of population configuration and others that outwardly appear to be metapopulations such as mainland-island and source-sink configurations (Harrison 1991). In the mainland-island configuration, most movement occurs from a larger patch to smaller patches. These metapopulations do not function in the "true" reciprocal colonization pattern unless the mainland population goes extinct (Thomas and Jones 1993) and is recolonized by the smaller "islands." In a source-sink metapopulation, the higher quality source habitat patch produces a surplus of descendants (rate of population growth or $\lambda > 0$), whereas the low quality patches may be sinks that produce a deficit ($\lambda < 0$) (Pulliam 1988, Pulliam and Danielson 1991).

Debate currently exists over how many examples of true metapopulations exist in nature (Harrison 1994). This may be due in part to the lack of studies that embody the spatial and temporal scales necessary for studying metapopulations.

Metapopulation Persistence

For a metapopulation to persist, the rate of patches being colonized and established must exceed the rate of patches going extinct (Levins 1970, Hanski 1989). A metapopulation is said to be at equilibrium when these rates are equal. Departures from equilibrium towards increasing extinction rate may ultimately result in a regional extinction. There may be a threshold number and configuration of occupied patches, below which the species is not likely to rebound (Hanski 1991), similar to the concept of a minimum viable population of individuals (MVP; Shaffer 1981).

Persistence of individual patches is determined by dynamics that occur both within the patch and by movements between patches. Population dynamics, internal to patch dynamics, such as natality, mortality, sex ratio, and age structure, interacting with patch size, habitat quality, and predator density determine the size of the local population and its variability.

Between-patch dynamics are shaped by a species' home range, spacing and movement patterns, especially dispersal. Movements between patches are

obviously important for patch colonization and establishment. These movements also may stabilize local population variability of occupied patches and increasing the persistence time for the local population through the rescue effect (Brown and Kodric-Brown 1977). Patch configuration and the type of habitat between the patches (including developed land) may ultimately have a large impact on the individual's movements.

At the scale of the entire metapopulation, the correlation in environmental variation among patches and the frequency of large-scale environmental catastrophes, is vitally important (Quinn and Hastings 1987, Gilpin 1988, Hanski 1989, Stacey and Taper 1992). If all patches are subjected to the same adverse environmental conditions at the same time, then patch extinctions may be correlated, leaving few or no source populations to colonize the extinct patches.

Additionally, the cause of local extinctions may be important to the overall metapopulation dynamics. It has been suggested (Thomas 1994) that most local extinctions are due to deterministic changes in the environment of a patch that render a patch unsuitable. If deterministic, these conditions are likely to persist following the local extinction leaving the patch empty, but unsuitable. Therefore, most empty patches are currently unsuitable for occupancy and few suitable patches become empty. Some populations, either because of their small size or inherently high variability, may be subject to

stochastic as well as deterministic forces of extinction. In these "turnover-prone" species (Schoener and Spiller 1987; Harrison 1991), empty patches of suitable habitat may be relatively common.

Dissertation Structure

This dissertation incorporates data on the Lower Keys marsh rabbit at 3 spatial levels of observation: within-patch population dynamics, inter-patch between population dynamics, and metapopulation dynamics. Using simulation models that incorporate these three spatial scales, predictions are made for a range of temporal scales.

Chapter 3 investigates the dynamics of 5 populations of Lower Keys marsh rabbits living in habitat patches. Estimates of natality, mortality, demographic structure, genetic and morphological variation were made at this scale. In Chapter 4, the home range size, movement patterns, and dispersal ability of the marsh rabbit were measured. This information about marsh rabbit inter-patch use provided the basis for testing the hypothesis that the marsh rabbits are existing in a true metapopulation configuration.

Chapter 5 explores patch occupancy, extinction, and (re)colonization at the metapopulation scale. Marsh rabbit diet, microhabitat, and macrohabitat selection were combined with the physical attributes of the patch to determine if these parameters influenced patch occupancy. Chapter 6 incorporates the

conclusions drawn from chapters 3-5 into a PVA to test the hypothesis that the metapopulation was in equilibrium. Predictions about the future for the Lower Keys marsh rabbit were made under a number of different scenarios.

In the final chapter (Chapter 7), conclusions and recommendations are made for the management and conservation of the Lower Keys marsh rabbit and other endangered species inhabiting patch/fragmented landscapes. Predator control, species reintroductions, the impact of more habitat loss, diseases, and the impact of hurricanes, are examined in light of the new research on metapopulation dynamics.

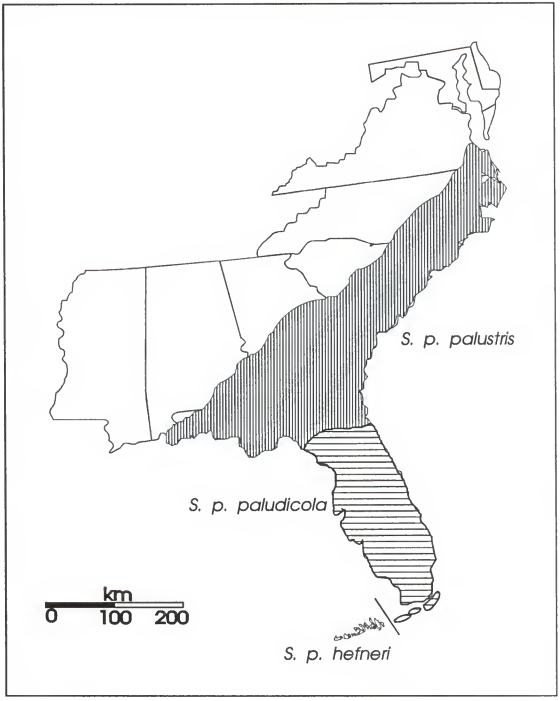


Figure 1.1--Distribution of the 3 subspecies of marsh rabbit (Sylvilagus palustris).

CHAPTER 2
THE LOWER KEYS OF FLORIDA

Geologic History

The Lower Keys of Florida are the terminal portion of an archipelago of islands extending westward from the mainland of Florida (Figure 2.1). For the purposes of this dissertation, the Lower Keys includes all of the islands from Key West to Noname Key (inclusive). The Lower Keys are separated from the Upper Keys by nearly 20 km of water (from Noname Key to Vaca Key).

The Keys are derived from coral reefs that formed during the Sangamon interglacial period (340,000-100,000 BP). During the subsequent Wisconsin glacial period, the Lower Keys were covered with oolitic sands and were gradually exposed as sea level began to fall. At the height of the Wisconsin glaciation (20,000 - 15,000 BP) the Keys were points of high relief amid the large land mass of Florida (Shinn 1988, Mueller and Winston 1991). At this point in time, Florida had nearly twice the exposed land as today (Webb 1990). Sea level remained low until nearly 15,000 BP, when the climate began to warm. Sea level rose rapidly from 15,000 - 10,000 BP, reaching a maximum of 7 feet/year, and then the rate slowed. During the past 2,000 years sea level has risen only 6 feet.

Today, the Florida Keys are composed of two formations of limestone. The Upper Keys (Soldier Key to the southeastern corner of Big Pine Key) are composed of the Key Largo limestone and the Lower Keys (the majority of Big Pine Key to Key West) are from the Miami limestone. The Miami limestone is composed of small ovoid pellets of calcium carbonate (ooids; Hoffmeister 1974) that hardened when sea level fell and the land surface was exposed to air.

Climate

Although several degrees north of the Tropic of Cancer, the close proximity of the Gulf Stream and maritime influences produce a subtropical climate in the Lower Keys (Chen and Gerber 1990). In 50 years of data collection, the temperature in the Lower Keys has never fallen below freezing, and the record low temperature is 41° F (5° C). Winter cold fronts are buffered by the warm ocean water before proceeding to the Keys. Monthly average temperatures differ only 15° F (9° C) from January to July (Figure 2.2). Daily temperatures rarely vary more than 10° F (12° C) between the high and low.

There are distinct dry and wet seasons in the Lower Keys, although this area is generally slightly drier overall than the Upper Keys and mainland Florida (Chen and Gerber 1990). The dry season spans November through April and accounts for less than a third of the annual precipitation. The

remaining two-thirds of the rainfall occurs during the wet season which begins in May and ends in October (Figure 2.2). Relative humidity remains high throughout the year, averaging nearly 75% (NOAA 1993).

Hurricane season occurs mainly during the wet season, from June until November. The chance that a hurricane (winds >74 mph) will hit the Lower Keys is slightly less than 10% each year. Historically, most hurricanes have occurred during the months of September and October. Tropical storms (i.e., winds 39-74) occur more frequently, but do not produce the large storm surges and destruction that hurricanes are capable of producing.

Flora and Fauna

The flora of the Lower Keys is derived from 4 sources: the Caribbean, the eastern U.S. coastal plain, endemic taxa evolved in place, and exotic taxa from cosmopolitan sources (Long 1974). Four plant associations predominate: mangrove, transitional salt-marsh, pineland, and hardwood hammock.

Mangrove community is dominated by 3 saline-tolerant, unrelated species: red mangrove (Rhizophora mangle), black mangrove (Avicennia germinans), and white mangrove (Laguncularia racemosa). These trees occur in areas that are either continually submerged or tidally inundated.

Transitional salt-marsh (also called the transition zone) is a grassy, nearly treeless marsh area that generally occurs from 1 to 3 m above sea level.

The majority of transition zone marshes are subject to predictable flooding by spring lunar high tides (Williams 1991). Transition zone marshes often occur between the mangrove community and the upland hardwood or pine hammocks. The transition zone can be further divided into two components: an open saltmarsh and at slightly higher elevations, a more forested area dominated by buttonwood (Conocarpus erectus). Several species of mammals, including the Lower Keys marsh rabbit inhabit this area.

On land where there are well-developed fresh water lenses, the pineland community can occur. These areas are rarely inundated by salt water and are maintained through periodic burns. Slash pine (Pinus elliottii) is the dominant tree species, although various species of palms and ferns are also abundant (Snyder et al. 1990). At the highest elevations (>3 m) the diverse hardwood hammock occurs (Carlson et al. 1992). This is the climax community in the Keys and occurs on nearly every large key. Nearly 10% of all tree species found in this area are endemic (Long and Lakela 1971).

Although less common, fresh water wetlands dominated by sawgrass (Cladium jamaicensis) do occur on the few keys that have a fresh water lens. A few keys also have limited amounts of beach and dune habitat, but most of the keys have exposed limestone rock on their coasts.

All of the native terrestrial mammals are derived from populations of the continental United States (Layne 1974). Currently, only 5 species of native

terrestrial mammals and perhaps 1 bat are found in the Lower Keys. All of the terrestrial mammals have been cited as being endemic in the literature at either the species or subspecies level (see Lazell 1989), although the accuracy of these taxonomic claims has been debated (see Humphrey 1994). The paucity of mammals in the Lower Keys may be related to the current isolation and small area of the Keys, combined with a lack of fresh water (Layne 1974).

Herpetofaunal diversity is greater than the mammals, although a large number of reptiles and amphibians in the Lower Keys are exotics (Wilson and Porras 1983). Of importance to the Lower Keys marsh rabbit, the eastern diamondback rattlesnake (Crotalus adamanteus) is common throughout the Lower Keys and the alligator (Alligator mississippiensis), although rare, does occur. Avian diversity, both breeding and over-wintering is fairly high in the Lower Keys although lower than mainland Florida (Robertson and Kushlan 1974). Special references to birds and reptiles as predators will be made in Chapter 3.

Development

By the 1890s Key West was the largest city in Florida and one of the largest in the United States. The remainder of the Keys were unpopulated until the completion of the overseas highway in 1938 and the first water pipeline in 1942 (Gallagher 1991). Today, over 78,000 people live in Monroe county,

nearly half of them in the Lower Keys (Shermyen 1993). The populations has increased nearly 65% since 1960. Tourism, which was also high during the late 1800s, has also resurged in the Lower Keys. At the 2 National Park beaches in the Lower Keys, over 500,000 tourists were recorded in 1993. The majority of these visitors came to the Lower Keys and Key West via the Overseas highway (Shermyen 1993).

Human impact on the Keys' wildlife was noticed as early as 1908, when the Key West National Wildlife Refuge was established to provide habitat for migratory birds. The Great White Heron National Wildlife Refuge was established in 1938, encompassing a collection of small islands north of the main chain of keys. In 1957, the National Key Deer Refuge was established; its main mission was to protect the Key Deer (Odocoileus virginianus clavium) and other wildlife. The largest tracts of land for this refuge are on Big Pine Key and Noname Key, but other areas on the Torch Keys are currently being added (John Andrew, National Key Deer Refuge Manager, pers. comm., 1993).

The United States military presence began in the Keys during the Civil War, and waxed and waned throughout the past century (Hambright 1991). Due to the Lower Keys' proximity to Cuba, the Caribbean, and open water ideal for training aviators, the U.S. Navy currently maintains a base in the Keys. The Navy owns a large amount of land on Key West, Boca Chica Key,

and North Saddlebunch Key. The U.S. Air Force manages the northernmost portion of Cudjoe Key.

Study Sites

This study attempted to encompass all possible marsh rabbit habitat throughout the Lower Keys, including saltwater transition-zone habitat and fresh water marsh areas. Habitat areas were located using information from Howe (1988) , aerial photographs and ground survey. Initially, a patch of habitat was considered isolated from another patch if the 2 areas were divided by a major road, airplane runway, or large body of water. As a general rule, patches of habitat <0.5 ha were not sampled, although some exceptions were made. A previous study of marsh rabbit home ranges (Payne 1975) found that no adult home range was <0.5 ha.

Fifty-nine habitat patches were identified throughout the Lower Keys (Appendix A); no habitat was found on Key West, the most densely human-populated Key. Twenty-seven habitat patches were found on Boca Chica, 25 of which were owned by the U.S. Navy. Four patches were examined at the Saddlebunch Keys; 2 of which were owned by the U.S. Navy. On Sugarloaf Key, 9 patches of transition zone habitat were found; 1 of which is owned by the U.S. Fish and Wildlife Service (USFWS), and other is owned by Monroe County. Two privately owned patches were found on Cudjoe, and 1 site

partially on U.S. Air Force land. One privately owned site was found on each of Summerland and Ramrod Keys. Big Torch Key had 2 privately owned sites and one site owned by the USFWS. Middle Torch had 2 sites, both of which were owned by the USFWS. Little Torch had 1 habitat patch and this patch was owned by the Nature Conservancy (TNC). Big Pine had 7 habitat patches: 3 owned by the USFWS, 2 privately owned, and 2 owned by the South Florida Water Management District (SFWMD). Noname Key had 1 USFWS-owned habitat site.

Additionally, habitat was found on several of the smaller islands that are part of the Lower Keys chain but that are only accessible by boats. Habitat patches were found on Annette and Porpoise Keys, both of which are small islets northeast of Big Pine Key. These islets are part of the Great White Heron National Wildlife Refuge. Transition-zone patches were observed on Big Munson Key and Saddlehill Key. Big Munson Key is south of Big Pine and is owned by the Boy Scouts of America, Inc. Saddlehill is southeast of Boca Chica Key and is privately owned. The search for habitat on other isolated islets was not complete; the existence of small patches of habitat on more distant keys is a possibility.

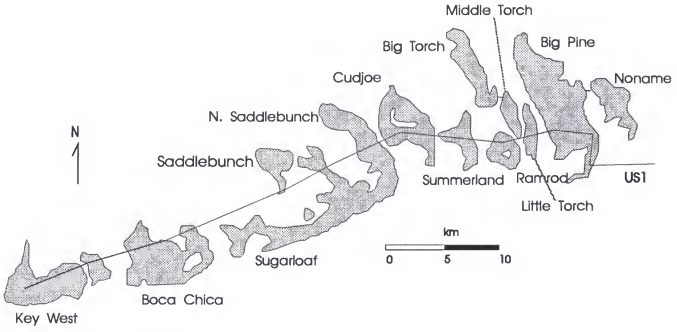


Figure 2.1--The Lower Keys of Florida. The solid line connecting the Keys is highway US-1.

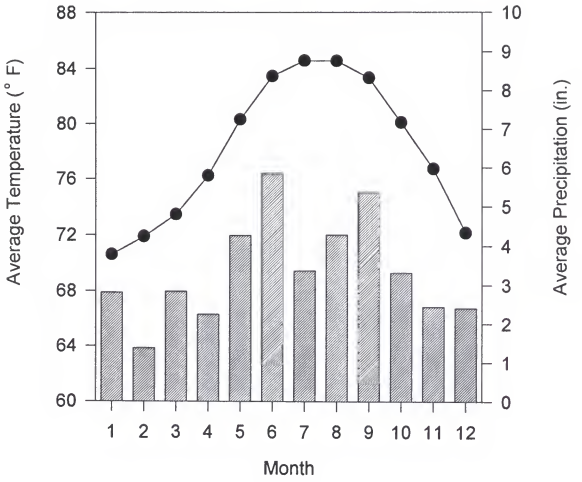


Figure 2.2--The average temperature (line, left axis) and average precipitation (bars, right axis) during the past 25(1965-1990) years measured at Key West airport, Key West, Florida.

CHAPTER 3
POPULATION BIOLOGY (INTRA-PATCH DYNAMICS)

Introduction

The first step in developing a population viability analysis (PVA) is determining the demographic and genetic composition of a population, how these compositions vary, and how large a role stochastic and environmental variability play (Salwasser et al. 1984, Gilpin and Soulé 1986). Demographic and genetic compositions of a population can influence population growth, variability in growth, and the ultimate population size, all of which can in turn influence the populations chance for persistence (Goodman 1987).

The demographic composition of a populations is determined by variation in the birth and death rates and in the sex ratio of the new recruits. Some variation in these parameters will be purely random, other sources of variation may be from external sources (i.e., differential mortality by sex or age group, biased sex ratios at birth), and therefore this variability may be correlated throughout the population. In a large, continuous population, random variations will contribute little to the overall population variability but environmental variability may be important; in very small, fragmented

populations, both stochastic and environmental variation can substantially alter sex and age ratios.

Genetic variability, at both the individual and population level, may also be important. Highly fragmented, isolated populations are at risk of loosing both types of variation. When a population is small and isolated, the chance of a mating between close relatives increases. These matings can produce young with a higher proportion of homozygous loci, thus potentially decreasing the number of heterozygous loci and increasing the number of deleterious recessive genes (Packer 1979). Certain heterozygous loci have been correlated with greater tolerance to environmental variations in some species (Lerner 1954).

This increase in homozygous deleterious genes, combined with a decrease of heterozygote loci, is believed to cause greater mortality, and reduced fecundity, creating a phenomena called "inbreeding depression" (see Lacy 1993). Loss of genetic variability among individuals or between populations may contribute to inbreeding depression, and may decrease the overall chance that the population can evolve to meet new environmental conditions. Although loss of genetic variability in insular populations is well documented (Kilpatrick 1981, Berry 1986) its overall effect on population persistence is less known.

Inbreeding depression was documented early in domesticated animals (Wright 1977, Falconer 1981), laboratory animals (Strong 1978) and more

recently in captively breed animals from wild stock (Ralls and Ballou 1983, Ralls et al. 1988). Evidence for inbreeding depression in natural populations is less clear (Lacy 1993), and in need of further study. Most examples of possible instances for inbreeding depression in the wild come from populations of large, long-lived species such as the grizzly bear (Ursus arctos; Harris and Allendorf 1989) and the Florida panther (Felis concolor coryi; Seal and Lacy 1989). These species have existed at extremely small numbers in the wild for several decades and have largely overlapping generations.

For smaller, shorter-lived species, it is currently hypothesized that before inbreeding depression can have an effect in the wild, habitat loss and demographic problems may have already caused the demise of the wild populations (Lacy 1993). Management for these problems may also help in preventing inbreeding depression and overall loss of genetic variability in the population, although more intense management may be needed for populations that have recently undergone severe population bottlenecks (Fuerst and Maruyama 1986). Inbreeding depression for these species may still be an important consideration in PVA, if captive breeding and reintroductions are available as management options (Haig et al. 1990).

The sensitivities of demographic and genetic compositions to random and environmental variation are dependent on the life history and population dynamics of the species in question. Further, they may be affected by

idiosyncratic factors such as the habitat available and climatic variation, and therefore require in-depth study.

Lagomorph population biology is characterized by high reproductive rates and high rates of mortality. All lagomorphs are entirely herbivorous, although they feed on a diversity of vegetation. Due to their high abundances and intermediate size, lagomorphs are the base of many predator-prey systems involving small to medium-sized predators (Chapman and Flux 1990).

Most research on rabbits has been on the most abundant species (e.g., eastern cottontail, Sylvilagus floridanus), primarily in relation to hunting. There is little information on the management of rare or endangered lagomorph species. Additionally, most research on endangered species (in general) has historically concentrated on larger species that are long-lived and have longer generation-times (Murphy et al. 1990). Threats to the persistence of smaller species with higher reproductive rates, but shorter life-spans (r-selected) will differ. These "r" selected species may be more habitat specific than "K" species and may experience higher variability in population numbers (Pimm 1991).

The objective of this portion of the research was to determine the demographic and genetic compositions of the Lower Keys marsh rabbit. Special emphasis was placed on parameters that affect the intrinsic rate of growth of the marsh rabbit populations (natality, mortality, sex and age ratios),

the variability of these parameters, and the extrinsic factors that influence this variability. This information about the population biology was used in the final model predicting the future of the Lower Keys marsh rabbit presented in Chapter 6.

Methods

Two methods were employed to study the population biology of the Lower Keys marsh rabbit: live-trapping and radio-telemetry. Marsh rabbits were studied at a subsample of 6 habitat patches. All of the patches chosen were on Navy-owned land; a diversity of patch size and shape was sampled. Five habitat patches were selected on Boca Chica and 1 on Saddlebunch Key. Additional sites throughout the Lower Keys were used for the portion of the study that examined the genetic composition of the marsh rabbits.

Trapping Grids

Individual marsh rabbits were examined by trapping the 6 main sites. Trapping occurred twice during the wet season (June - November), and twice during the dry season (December - May). For the 5 sites on Boca Chica Key (Figure 3.1), trapping occurred from June 1991 to May 1993 (8 trapping sessions). On Saddlebunch, trapping was conducted from June 1992 to May 1993 (4 trapping sessions). Trapping grids were placed on each site, using

unbaited collapsible National live traps (80 x 30 x 30 cm), placed in a 6 x 6 array, spaced approximately 25 m apart. Each trapping session consisted of 5 nights where the traps were open, 2 nights with the traps closed and another 5 nights with traps open. Traps were checked twice daily, once in the morning and once in the evening and were covered in burlap for shade.

All rabbits caught were sexed, weighed, and tagged (Monel no. 3, National Band and Tag, Newport, KY). Measurements were made of the right rear foot, ear length from notch, and total body length from nose to (and including) tail. Marsh rabbits are relatively easy to sex (Nagy and Haufler 1980), but an aging method has not been determined. An attempt to correlate weight, total length, ear length, and rear right foot length with age was made. Rabbits were classified as juveniles (not sexually mature), subadults (entering sexual maturity), or adults (fully sexually mature).

Genetic Analysis

Blood samples were obtained from all animals caught on the 6 trapping grids between June 1992 and May 1993. In addition, blood was taken from animals caught during preliminary trapping on Sugarloaf and Big Pine Keys. Blood samples were obtained by lancing the ear with a hypodermic needle and collected using heparinized capillary tubes. Blood was stored on wet ice for <1 hour and was centrifuged into plasma and hemolysate at 5,000 rpm for 10 min

(Scribner et al. 1983). The plasma and hemolysate were stored in liquid nitrogen and were analyzed used starch-gel electrophoresis within 1 year.

Eleven presumptive genetic loci were scored for the samples. Standard procedures for starch-gel electrophoresis were used (Harris and Hopkinson 1976). Locus nomenclature followed McAlpine et al. (1985) for mapped human genes. Two buffer systems were used. Tris-citrate, pH 6.7 was used for the following enzymes: esterase, E.C. 3.1.1.1 (EST-1); glucose phosphate isomerase, E.C. 5.3.1.9 (GPI); isocitrate dehydrogenase, E.C. 1.1.1.42 (ICD-1); lactate dehydrogenase, E.C. 1.1.1.27 (LDH-1), malate dehydrogenase, E.C. 1.1.1.37 (MDH-1); mannose phosphate isomerase, E.C. (MPI); and superoxide dismutase, E.C. 1.15.1.1 (SOD-1). Tris citrate, pH 8.0 was used for the following enzymes: beta hemoglobin (βHb); glutamate oxaloacetic transaminase, E.C. 2.6.1.1 (GOT-1); peptidase, E.C. 3.4.13 (PEP-1); and phosphoglucomutase, E.C. 2.7.5.1 (PGM-1).

Radio-telemetry

Each rabbit weighing >1,000 grams trapped at the 5 Boca Chica sites and the Saddlebunch site was fitted with a radio-collar (weight <3 grams) and a transmitter with an estimated 10-month operational life (Telonics, Inc., Mesa, AZ). Smaller rabbits (300-1,000 g) were fitted with a similar radio-collar, but with a velcro break-away device added to allow the animals to lose the

equipment as their bodies grew larger. Collars were replaced as the animals aged. Previous studies on cottontail rabbits (S. floridanus) found that mortality rates were not statistically different for radio-telemetered rabbits and rabbits marked using other methods (Trent and Rongstad 1974, Rose 1977).

Collared rabbits were located on separate days three times a week, once in the early morning (7-9 a.m.), once at mid-day (11 a.m. - 1 p.m.), and once in the evening (4-6 p.m.). Signals were followed until the animal could be seen or the exact location was found. All locations were made $\geq$24 hours apart to ensure independence of observations. Locations were plotted on 1:2400 aerial maps with 10-m^2 grid overlays. Because the 5 sites on Boca Chica were studied for 2 years and the Saddlebunch site was only studied during the final year, natality and mortality portions of the study only used data from the 5 sites on Boca Chica Key (Figure 3.1).

Natality

Natality was studied by examining females during each trap session for pregnancy (by palpating the uterus) and lactation. Nesting was determined by following collared female rabbits until they centered their activities around one small area. Nest confirmation was made by observing the young through a tunnel in the grass or by finding deposits of juvenile pellets near the nest area. Where possible, the number of young observed in or fleeing the main chamber

of the nest was recorded. Although this method is approximate, it provided an estimate of the number of individuals surviving at the time of nest discovery. Number of litters for each female was calculated for both the wet and dry seasons and compared using a likelihood-ratio Chi-square (G^2). The nest area was mapped, and the dominant vegetation was identified.

Mortality

Percent mortality was calculated for 5 age classes: nestling, juvenile, subadult, first-year adult, and second-year adult. Nestling mortality (0-3 months) was calculated by comparing the number of young observed in nests to the number of juveniles caught on the trapping grid. Juvenile mortality (4-7 months) was estimated using telemetry for individuals >300 g. Subadult (8-10 months), first-year and second-year adult mortality was determined from the telemetry data alone. First-year adults were rabbits that had been followed as an adult for 1 year; most had been collared as juvenile or subadults. Second-year adults were rabbits that had been followed as adults for 2 years. First- and second-year adult classes may have contained individuals older than 2 and 3 years old.

All mortalities were located within 2 days of death. When possible, field necropsies were performed as outlined by Wobeser and Spraker (1980),

with special attention to the liver for signs of tularemia (Francisella tularensis). Site description, carcass condition, and position was recorded for each death.

All rabbit carcasses thought to have been preyed upon were examined for signs of trauma. The head, throat, and neck were examined for puncture wounds. Hemorrhaging, particularly the presence of blood in the mouth, nares, trachea or neck region indicated the rabbit was alive at the time of attack (Hawthorne 1980). Feeding pattern on the carcass was also examined: hindquarter feeding probably indicated scavenging, whereas feeding on the shoulders and neck indicated possible predation (Hawthorne 1980).

When predation was suspected, the site was examined for sign on and around the carcass. Tracks and scats were identified for potential information on the predator or scavengers. Potential predators found in the Lower Keys included Bald Eagles (Haliaeetus leucocephalus), Red-shouldered Hawks (Buteo lineatus), eastern diamondback rattlesnakes (Crotalus adamanteus), feral cats (Felis catus), raccoons (Procyon lotor) and possibly Black Vultures (Corgyps atratus) and domestic house-based dogs (Canis familiaris).

Birds of prey tend to capture rabbits in the middle of the back, and will kill using deep puncture wounds to the back and head (Hawthorne 1980). They may take their prey back to a nesting area. Feral cat predation may be assumed if the carcass has been dragged, eviscerated, or covered in dirt. Often cats will leave tooth marks on every exposed bone of their prey (Anderson

1969). Raccoons are more likely than cats to eat the breast, crop, and entrails of their prey. They may also carry portions of the prey to water (Anderson 1969).

Results

A total of 54 Lower Keys marsh rabbits was caught and examined during this study (Table 3.1). Forty-three were caught on the 6 main grid sites (41 on Boca Chica, 2 on Saddlebunch), 5 rabbits were caught while trying to recapture collared dispersed rabbits, and 6 were caught on other sites in the Lower Keys. Rabbits were only examined once per trapping period. Data from the 54 rabbits was recorded 130 times during 8 trapping sessions (June 1991 - May 1993).

Forty-three (28 male, 15 female) of the rabbits caught were fitted with radio-collars, and 7 of these were juveniles. More juveniles were caught before the break-away collar technology was complete. Forty-one of the radio-collared rabbits were on Boca Chica Key and two were on Saddlebunch Key.

Growth and Morphology

Mass of the 54 marsh rabbits ranged from 100 to 1400 grams (including pregnant females). It was judged that the 100-gram rabbits had just left the nest and were approximately 1 month old. Several young rabbits were causght,

but only 3 rabbits (1 male, 2 females) were caught during this stage and survived to adulthood. Marsh rabbit age was correlated with external measurements using these 3 individuals.

Both body mass and total body length were found to significantly ($P < 0.05$) predict marsh rabbit age for all 3 rabbits (Table 3.2). Ear length and the length of the right hind foot were not significant predictors in one of the female rabbits. Body mass has been used as an indicator of age in cottontails (Lord 1963), but the length of the right rear foot is used more often (Bothma et al. 1972). Because measuring the length of a non-sedated marsh rabbit is difficult, the marsh rabbit body mass was used as an indicator of age in conjunction with appearance of external sexual organs. Body mass can be influenced by nutritional and physiological variations but was the most objective and accurate age indicator available. Body mass of the marsh rabbits increased almost linearly with age for the 3 rabbits and plateaued at approximately 1,100 grams (Figure 3.2) as the rabbits approached 1 year.

External measurements collected from 13 non-pregnant adult female rabbits and 19 adult male rabbits were compared for differences using a Wilcoxon test. In an attempt to use only measurements on fully grown rabbits, only individuals that had been caught more than once as an adult were used. No significant differences were found in any of the measurements between sexes. Approximately half of all cottontial species are sexually dimorphic

(females larger) and the other half exhibit no dimorphism (Champman et al. 1982). The average measurements and standard deviations of 29 marsh rabbits were as follows: mass 1224.1 g. (80.9), total length 339.3 mm (24.9), ear from notch 52.7 mm (3.4), and right hind foot 73.6 mm (3.7).

Genetics

Two (EST-1 and PGM-1) of the 11 loci sampled from the 19 rabbits were polymorphic, indicating that there is genetic variation in the Lower Keys marsh rabbit (Table 3.4). This proportion of variable loci is only slightly less than the proportions seen in studies of cottontail rabbits in Texas (Scribner and Warren 1986). Deviations from Hardy-Weinberg expectations were not observed ($P > 0.05$) at either of the polymorphic loci, but this test may not be valid on a so small sample. Differences in allelic proportions for each locus appeared to vary among keys, but sample sizes were too small for statistical comparison. Heterozygous loci and variation among individuals occurred at Boca Chica, Geiger, and Sugarloaf Keys. The 2 rabbits sampled on the Navy land on Saddlebunch Key were homozygous and monomorphic at all loci. Only 1 individual was sampled from Big Pine Key; this individual was heterozygous only at the EST-1 loci and contained an allele at the EST-1 locus that was not seen at any of the other keys.

Demographics

The number of marsh rabbits caught on the 5 main sites varied from a high of 18 rabbits during November 1991 and February 1992 to a low of 9 during November 1992 (Figure 3.3). The small number of rabbits at each site precluded the use of capture/recapture statistics (Pollock et al. 1990); population number at each site was estimated using the minimum number known alive (MNA; Hilborn et al. 1976).

When all of the male and female individuals caught over the 8 trapping sessions at the 5 Boca Chica sites were counted, there appeared to be more male than female rabbits on the 5 sites during the study (Table 3.3). The sex ratio significantly male-biased in only the subadults; nearly equal numbers of male and female juveniles and adults were captured on the 5 grids.

Trappability (the probability that a rabbit was captured more than once during the 10-day trapping session) differed among the demographic groups (Table 3.5). Male and female trappability was high and not statistically different. Juvenile trappability was lower, and females were more likely to be retrapped during a trap session than were males. Subadult trappability was high for the males, and very low for females. Sample sizes for the trappability comparisons were small.

Natality

Eleven adult female marsh rabbits were radio-collared, followed for >1 month, and used in this portion of the analysis. Length of time followed ranged from 2 to 22 months ($\underline{X}$ = 9.09 months, $\underline{SE}$ = 1.94) for a total of >100 months. Thirty-one nesting events were recorded; all females were observed to nest and produce a litter at least once. The number of young observed per nest ranged from 1 to 3 with an average of 1.77 kittens per nest ($\underline{SE}$ = 0.09).

All nests were made in clump grasses (thick grasses and sedges), with 22 of the nests predominately in Spartina spartinae and the other 9 in Fimbrystylis castanae. In general, the nests consisted of a main chamber with several smaller chambers and exit/entry routes. None of the nests were obviously lined with fur as reported in the northern subspecies (Tomkins 1935). Only 2 of the females used the same nesting area more than once, and none of the female rabbits used the nest of another rabbit during this study.

There was little apparent seasonal pattern in the reproduction of the marsh rabbit (Figure 3.4). Combining data from the 2 years of the study, the proportion of rabbits that produced litters each month ranged from 0-56%. The highest proportion of females with litters was seen in March and September; the lowest proportion was seen in April and December. The average number of litters produced during the wet and dry seasons did not differ significantly ($\underline{G}^2$ = 0.15, $\underline{df}$ = 1, $\underline{P}$ > 0.05). Although reproduction in most cottontail species is

highly seasonal (Chapman et al. 1982), reproduction in marsh rabbits in southern Florida (Holler and Conaway 1979), southern Texas (Bothma and Teer 1977), and southern California (Ingles 1941) exhibits only year-round slight seasonal fluctuations.

Time between litters ranged from 1 to 5 months ($\underline{X}$ = 2.45, $\underline{SE}$ = 0.30). Combining the results from the 11 rabbits, an average of 3.7 litters per year was produced. Although their research methods differed from those reported here, Holler and Conaway (1979) measured a higher fecundity rate (5.7 litters per year) for marsh rabbits (S. p. paludicola) living in southern Florida.

Mortality

Fiftythree rabbit kittens observed in the nests, but only 15 young rabbits were trapped on the grids. The survival rates (from one developmental stage to the next) at the 5 main study sites ranged from 13 to 50%. Forty-one individuals (26 male, 15 female) were trapped and collared at the 5 sites on Boca Chica Key. Twenty seven (19 male, 8 female) died during the study. Because of these small sample sizes in some of the demographic groups statistical tests were not used. Percent mortality was highest for the second year adults ($\underline{X}$ = 90%) and lowest for the juveniles ($\underline{X}$ = 25%). Male mortality (%) was higher than female mortality for each age class (Figure 3.5). None of the females in the study died during their subadult period, but nearly half of the

subadult males were killed. One female was caught as a subadult and then followed until the study ended, establishing a maximum longevity of 3 years for this study.

Cause of mortality was determined for 24 rabbits (Figure 3.6). None of the juvenile mortalities were included because their bodies were never found. Presence of blood and fur on the break-away collar and subsequent disappearance from the trapping grid were assumed to mean the animals had been killed. It was possible to determine the cause of mortality for all of the subadults (all male) and 19 of the adults. Only 1 of the adults disappeared during the study.

Cause of mortality was organized into 6 classes: cat/raccoon, vehicle, rattlesnake, raccoon, cat and poaching. The cat/raccoon class was used for mortalities where it was not possible to distinguish between predation by a feral cat or raccoon. Sign from both predators was abundant at the kill sites. In nearly all of the kills the rabbit was dragged and partially buried, indicating cat predation. In 3 cases the cat or raccoon was seen with the rabbit, and it was assumed that the predator had killed the animal. In addition, Arnim Sheutz (the Natural Resource Manager for the Navy on Boca Chica Key, pers. comm.) reported an observation oft a Bald Eagle grasping a medium-sized marsh rabbit.

Full necropsies were only possible on 2 of the rabbits. The remainder of the carcasses were entirely eaten, eviscerated, or decomposed. Neither of the necropsies revealed any sign of disease.

The most subadult and adult mortalities were caused by vehicles (Figure 3.6). It was followed closely by the number of individuals killed by feral cats and raccoons. Three rabbits were eaten by rattlesnakes (the radio-collar transmissions were traced to the rattlesnake) and one rabbit was shot. Both sexes appeared to be susceptible to predation by cats and raccoons, but more males were killed by vehicles. Seven males were killed by vehicles on the road, 4 of them subadult males. The only female road-kill was actually killed in the marsh adjacent to the road. The vehicle had apparently been driven through the habitat. Mortality on and off the base on Boca Chica Key was similar. Road-kills, feral cat predation, and raccoon predation occurred on both on and off the base on Boca Chica Key. All of the predation by rattlesnakes and the poaching occurred on Navy land off the Boca Chica base.

Discussion

The high recapture rate of adult marsh rabbits indicates that most adult rabbits living on a grid were probably captured during the study. The lower trappability percentages for juveniles and female subadults suggests that some of these individuals might have been missed. Because of this difference in

trappability, most notably in the female subadults, the apparent male bias in the sex ratio may be due to differences in the trappability. Both male and female biased sex ratios are common in the literature (Chapman et al. 1982). Speculation about the role of biased sex ratios of litter and of adult rabbits has been made in relation to mating systems (Chapman et al. 1977), population density, precipitation, and success of hunters (Edwards et al. 1981).

Average productivity for female Lower Keys marsh rabbit (6.36 young/year) was slightly lower than for marsh rabbits in southern Florida (Holler and Conaway 1979). However, the productivity measure in this study only accounts for young seen in the nest during a 2-week period after birth. It is possible more young were born and not seen in the nest or that some young died before, during, or shortly after birth. Productivity estimates are substantially lower than for eastern cottontail rabbits (Chapman et al. 1982). Lord (1960, 1963) noted that a decrease in the litter size of cottontails was correlated with a decrease in latitude. As the size of the litter decreases, the potential length of the breeding season increases. The breeding season and litter size of the Lower Keys marsh rabbit are consistent with this general observation.

Breeding was year-round in the Lower Keys. Cottontail breeding and reproduction are generally tied to temperature and precipitation. In the Keys, these climatic changes may be more subtle. Although the Florida Keys lie a

few degrees north of the Tropic of Cancer, the climate can be considered tropical (Walter et al. 1985). The temperature in the Lower Keys has not fallen below freezing in historic times. Rainfall is seasonal, but the Keys do receive one-third of their rainfall during the "dry" season. Slight variations in marsh rabbit reproduction might be related to inter-year variation in precipitation.

Marsh rabbit mortality was high for nearly every age class and sex. The estimate of nestling mortality, however, may be negatively biased. The probability of catching a rabbit during the first 3 months of its life is unknown and it is possible that some young rabbits survived the first 3 months but were killed later as juveniles. It seems unlikely that the young rabbits left the habitat patch. Cottontail rabbits are extremely altricial, and very young rabbits appear to be only capable of moving short distances, especially without cover.

Subadult males appeared to have a particularly high mortality rate, mainly due to the number killed by vehicles. Second-year adults also have a high mortality rate, indicating that adult marsh rabbits may become more vulnerable to predation as they age. In general, fewer females were killed than males. This difference in mortality data may be due to the male-skewed sex ratio of the radio-collared subadult rabbits.

Vehicles killed nearly a quarter of radio-collared marsh rabbits in this study, including the subadult dispersing males. Because marsh rabbits are most active from dusk until dawn, night-time road traffic appears to be a threat to

marsh rabbit survival. Predation by cats has not previously been reported for marsh rabbits, but cats were a major predator of adult and juvenile rabbits of other species in several other studies (Fitzgerald and Karl 1979, Jones and Coman 1981, Liberg 1985). The cat population of the Lower Keys is large and includes feral and house-based cats.

Genetic Threats to Persistence

The Lower Keys marsh rabbit had a level of variation similar to large populations of cottontails (Scribner and Warren 1986). Inbreeding depression does not appear to be a threat for most of the Lower Keys marsh rabbits. Although past levels of genetic variation are unknown, it does not appear that these marsh rabbits are currently deficient in genetic variation. Future threats may be dependent on the population size and structure.

Demographic Threats to Persistence

Fecundity of the Lower Keys marsh rabbit is lower than other subspecies of marsh rabbits and other species of cottontails. Possible explanations for this lower fecundity include: reabsorption of fetuses (Holler and Conaway 1979), insufficient food or nutrients for reproduction (Cheeke 1987), adaptive pressures that have resulted in longer periods between pregnancies, and lack of suitable mates at the habitat patch.

Although the other hypotheses cannot be eliminated, it is highly probable that some females were without mating opportunities during part of the study. The low population density, combined with stochastic variation in the sex ratio of the adults at a habitat patch, left at least 2 females (sites 8 and 9, trapping period one) without mates. These females did not produce a litter during this period. The ability of males and females to travel between habitat patches will be examined in Chapter 4. If these habitat patches are separate populations, it appears that stochastic demographic variation can have a large impact on the intrinsic rate of growth of the population (r).

This lower fecundity was matched with a mortality rate higher than most non-hunted populations of wild rabbits (Trent and Rongstad 1974, Chapman et al. 1982). The majority of the mortality was from anthropogenic sources (vehicles, house cats), that are not generally density-dependent.

Table 3.1--Number of Lower Keys marsh rabbits (Sylvilagus palustris hefneri) trapped at each site in the Lower Keys of Florida from June 1991 to May 1993.

Site	Ownership	Male	Female	Total
3	Navy	1	0	1
4	Navy	2	1	3
7[a]	Navy	4	3	7
8[a]	Navy	8	4	12
9[a]	Navy	6	3	9
10[a]	Navy	4	1	5
13[a]	Navy	4	4	8
16	Navy	1	0	1
19[b]	Navy	2	1	2
22	Private	1	2	3
34	USFWS[c]	1	2	3

[a] One of the 5 main study sites.
[b] The Navy-owned Saddlebunch site.
[c] United States Fish and Wildlife Service.

Table 3.2--Correlation coefficients between body mass, body, ear, and right foot length and rabbit age for three Lower Keys marsh rabbits (Sylvilagus palustris hefneri). In parenthesis are the number of times each rabbit was examined.

Trait	Female #1 (N=4)			Female #2 (N=5)			Male #1 (N=5)		
	R^2	F	P	R^2	F	P	R^2	F	P
Body mass	0.97	70.1	0.01	0.97	84.1	0.01	0.90	18.6	0.05
Body length	0.93	27.0	0.04	0.94	49.7	0.01	0.94	29.5	0.03
Ear length	0.80	8.2	0.10	0.96	71.8	0.01	0.91	19.4	0.05
Right foot length	0.82	8.9	0.10	0.93	41.1	0.01	0.92	22.6	0.04

Table 3.3--The number of sexually mature Lower Keys marsh rabbits (Sylvilagus palustris hefneri) at the 5 main study sites on Boca Chica Key.

Session		Site					
		7	8	9	10	13	Total
1	Male	0	0	0	1	1	2
	Female	0	1	1	1	2	5
2	Male	0	1	0	1	1	3
	Female	0	1	1	1	2	5
3	Male	2	2	1	1	1	7
	Female	2	1	1	1	2	7
4	Male	2	1	1	1	1	6
	Female	2	2	1	1	1	7
5	Male	2	1	3	1	2	9
	Female	1	1	1	0	1	4
6	Male	1	2	1	1	1	6
	Female	1	2	2	0	1	6
7	Male	1	1	1	1	1	5
	Female	0	1	1	0	1	3
8	Male	1	0	1	1	1	4
	Female	1	0	2	0	2	5

Table 3.4--Allele frequencies for all variable loci[a] among 5 marsh rabbit populations (Sylvilagus palustris hefneri) from the Lower Keys of Florida, June 1992 - May 1993. Individuals were trapped on sites 7, 8 and 9 from Boca Chica, sites 10 and 13 from Geiger Key (the southeastern portion of Boca Chica), site 30 on Saddlebunch, site 33 on Sugarloaf, and site 53 on Big Pine.

		Site (N)				
Locus	Allele	Boca Chica (9)	Geiger (5)	Saddlebunch (2)	Sugarloaf (2)	Big Pine (1)
EST-1	A	0.389	0.200	1.000	0.250	
	B	0.611	0.800		0.750	
	C					1.000
PGM-1	A	0.778	0.500	1.000	0.500	1.000
	B	0.222	0.500		0.500	

[a]The following loci were assayed but were monomorphic: GOT, GPI, Hb, ICD-1, LDH-1, MDH-1, MPI, PEP-1, SOD-1.

Table 3.5--The sum of all marsh rabbits (Sylvilagus palustris hefneri) trapped at the 5 main sites on Boca Chica during the 8 trapping sessions (June 1991 to May 1993), and the proportion of these rabbits that were trapped twice during a 10-day trapping session. The G^2 for the "number" indicates a test to determine if the sex ratio of the trapped rabbits differed from 1:1. TheG^2 for the "trappability" indiciates a test to determine if the trappability differed between sexes.

Age	Male		Female		Male:Female	
	Number	Trappability	Number	Trappability	Number G^2	Trappability G^2
Juvenile	8	50%	6	67%	1.0	11.6*
Subadult	14	71%	4	25%	14.3*	59.6**
Adult	42	83%	42	88%	0.0	0.6

* $P < 0.05$

** $P < 0.001$

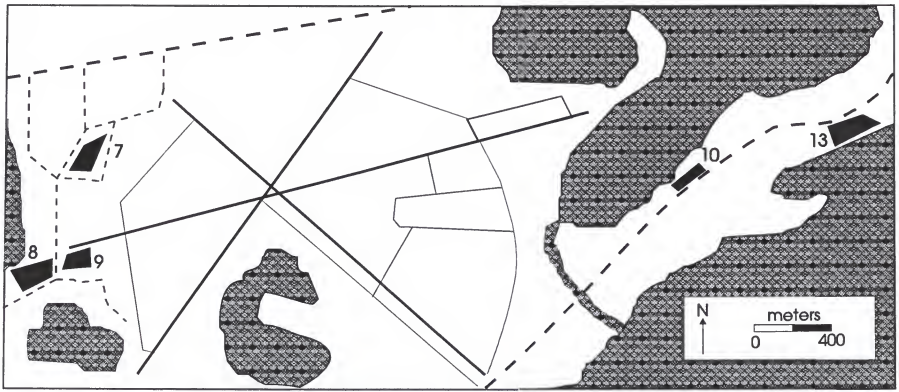


Figure 3.1--Five main habitat patches on Boca Chica used for trapping and radio-collaring of Lower Keys marsh rabbits (Sylvilagus palustris hefneri). The solid lines are runways and taxiways. The dashed line are roads.

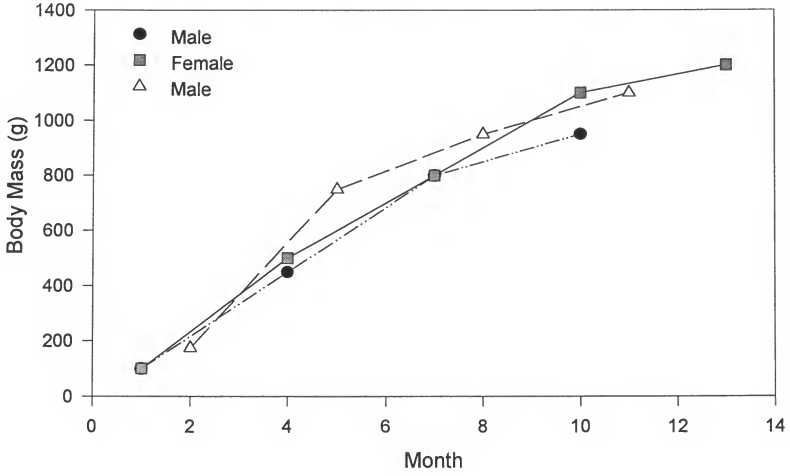


Figure 3.2--Growth curves for 3 (1 male and 2 female) Lower Keys marsh rabbits (Sylvilagus palustris hefneri).

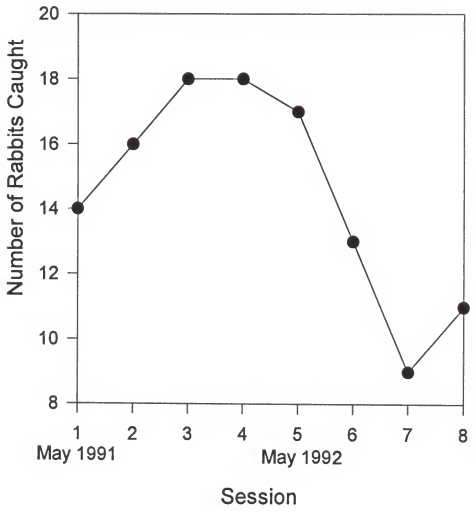


Figure 3.3--The number of Lower Keys marsh rabbits (Sylvilagus palustris hefneri) caught during each trap session at the 5 main sites.

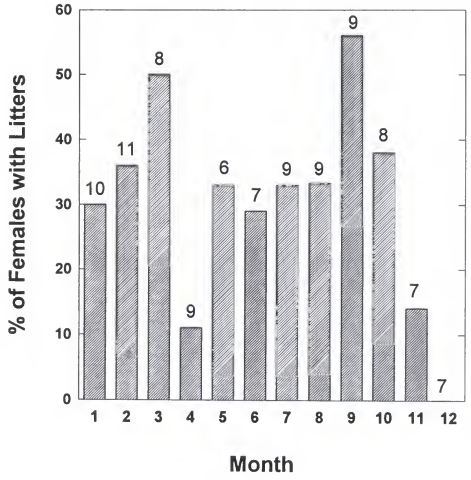


Figure 3.4--Proportion (bar) and number (above bar) of Lower Keys marsh rabbits (Sylvilagus palustris hefneri) that produced a litter during each month. Data from 2 years were combined and averaged. (January = month 1, December - month12).

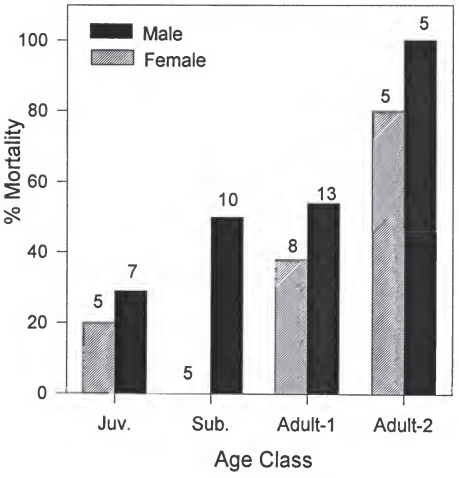


Figure 3.5--Percent mortality of Lower Keys marsh rabbits (Sylvilagus palustris hefneri) by sex and age class. Sample size of each age/sex cohort is indicated above each bar.

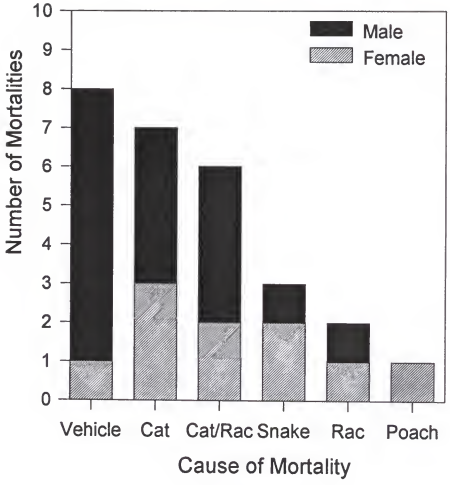


Figure 3.6--Cause of death for 24 Lower Keys marsh rabbits (Sylvilagus palustris hefneri). (Vehicle - car, truck, or plane; Cat = domestic cat; Cat/Rac = unable to distinguish if predator was a cat or a raccoon; Snake = eastern diamond back rattlesnake; Rac = raccoon; Poach = death by gun)

CHAPTER 4
SPATIAL ORGANIZATION (INTER-PATCH MOVEMENTS)

Introduction

To apply knowledge about the Lower Keys marsh rabbit's population biology in a PVA, it is necessary to define the unit of individuals that comprises a local population. A local population can be loosely defined as a set of individuals that has a high probability of interaction (Hanski and Gilpin 1991). Local populations may be part of a greater metapopulation where interaction occurs via individuals moving among populations (Levins 1970).

The unit of the local population can be determined by studying the spatial structure and movements of individuals at different spatial scales. An individual's home range, spacing behavior, and movements (including dispersal) will determine the spatial scale of interaction with others. These behaviors may vary among individuals of different sexes and ages.

The home range of an individual is the area used for foraging, mating and caring for young (Burt 1943, White and Garrott 1990). It does not include areas used in migrations, or other occasional round-trip excursions. Home range is calculated using a variety of methods that take periodic readings on an individual's location.

Home-range size varies greatly among individuals, populations and species of the genus Sylvilagus (see Chapman et al. 1982); Only 1 study has attempted to estimate home-range size for the marsh rabbit (S. palustris). Blair (1936) estimated a "linear home range" based on a maximum home range width of 183 m from trapping data.

It is generally assumed that most cottontails are not territorial (Chapman et al. 1982). This assumption is based largely on studies of the eastern cottontail (S. floridanus; Haugen 1942; Chapman and Trethewey 1972, Dixon et al. 1981) and the brush rabbit (S. bachmani; Shields 1960, Chapman 1971). Yet, Trent and Rongstad (1974) reported that female eastern cottontails did not have overlapping home ranges during the breeding season. Jurewicz et al. (1981) found small amounts of overlap in the nocturnal home ranges of breeding female eastern cottontails, and suggested that a spacing mechanism was in operation. Male swamp rabbits (S. aquaticus) have exhibited linear dominance hierarchies involving non-overlapping, defended home ranges in several studies (Marsden and Holler 1964, Sorenson et al. 1968, Holler and Sorenson 1969). Additionally, Kjolhaug and Woolf (1988) found no overlap between individuals of the same sex in both male and female swamp rabbits. Information on the spacing behavior of the other 10 species of cottontails (genus Sylvilagus) is lacking.

In addition to home-range size and spacing, it is also important to determine which habitat features a rabbit incorporates into its home range and which features act as barriers. Rabbits generally move while under vegetative cover (Chapman 1971, Trent and Rongstad 1974), probably to avoid predation. Large open areas are generally seen as barriers or at least deterrents to rabbit movements. Although the response of cottontail rabbits to roads and vehicular traffic has not been directly studied, field studies have found that improved roads (2-lane and larger) can be a barrier to small mammal and hare movements (Oxley et al. 1974, Mader 1984). Other possible barriers to rabbit movements include disturbed or developed areas with no natural vegetation, vegetated areas with insufficient cover, and open bodies of water. The marsh rabbit and the swamp rabbit are both known to be good swimmers (Svihla 1929, Tomkins 1935), although the frequency of swimming is not known.

While most rabbits stay within their home range and make few long-distance movements, young, subadult male rabbits have been documented traveling longer distances (Shields 1960, Chapman and Trethewey 1972). It is believed that these males are natal dispersers. Natal dispersal is male-biased in most polygynous mammals (Dobson and Jones 1985). Determining which sex disperses in a species and what factors motivate these movements are essential to understand a species' spatial organization.

Currently there is debate over the causes of natal dispersal (Dobson and Jones 1985, Pusey 1987, Wolff et al. 1991). Most research has been directed on determining the costs and benefits of dispersal to the dispersing individual. Three main hypothesis have been proposed: inbreeding avoidance, competition for mates, and competition for environmental resources (Packer 1979, Greenwood 1980, Dobson 1982, Greenwood and Harvey 1982). Different predictions for each hypothesis have been made, but research on a diverse sample of mammalian species has not been able to falsify any of the hypotheses. Two of the hypotheses, inbreeding avoidance and competition for mates are not mutually exclusive in their predictions. It has been proposed that the causal agents for dispersal may differ among species (Dobson and Jones 1985).

Recently, an alternative hypothesis has been proposed. Anderson (1989) has suggested that the focus should be on the fitness the resident (non-dispersing) adults receive by forcing the young to leave. In most polygynous mammals generally the father would receive the greatest benefit by coercing his son to leave. Although some evidence of dominants evicting subordinates exists in the literature (Moore and Ali 1984), other hypotheses can not be eliminated (Pusey 1987, Wolff et al. 1991).

Determining what direction and what type of habitat dispersing individuals will traverse are especially important in fragmented environments.

Two general theories have been proposed to predict the direct an individual will leave a patch. The random walk theory (Berg 1983) predicts that individuals will disperse across random locations along the edge of a patch, irrespective of habitat features. Patch geometry models (Stamps et al. 1987, Buechner 1989) predict that individuals will exit patches at more "permeable" areas. A landscape corridor may increase the patch edge permeability by extending patch habitat (La Polla and Barrett 1993), and allowing individuals to move from one habitat patch to another. The geometric and habitat features that constitute a "corridor" from the animal's perspective must be determined.

The objective of this part of the study was to use the information about the spatial organization of S. p. hefneri and movements to determine how they use the fragmented habitat in the Keys. Evidence supporting the hypothesized patterns of spatial use will be evaluated. Three possible scenarios of habitat use will be considered:

1. The Lower Keys marsh rabbit is confined to one habitat patch and is incapable of moving between patches. All home ranges occur strictly within the patch. Dispersal is within the patch, does not occur, or is unsuccessful (rabbit leaves a patch but does not reach another patch and dies or fails to reproduce). This will be called a "relictual" (Berry 1986) population.

2. Lower Keys marsh rabbits spend most of their lifetimes in a patch but are capable of moving between patches. All home ranges occur strictly

within the patch and individuals only interact with others living at the same patch. There may be occasional movements between patches and/or some of the dispersing individuals will successfully move to new patches. The areas surrounding the patches act as a barrier to most movements and is not included in the home range of the individuals. These patches contain sub or local populations that exist within a greater metapopulation (Levins 1970). These patches are not necessarily genetically distinct but are demographically isolated. Matings between individuals at different patches does not occur.

3. Lower Keys marsh rabbits move regularly between patches and may use several patches at once. The home ranges encompass several patches at one period of time and individuals interact with others from other patches regularly. All of the patches are part of one large population, which inhabits a highly fragmented environment.

Methods

Marsh rabbits were trapped at the 5 main sites on Boca Chica. Trapping occurred twice during the wet season (May - October), and twice during the dry season (November - April) from May 1991 to May 1993 (8 trapping sessions). Trapping grids were placed on each site, using unbaited collapsible National live traps (80 x 30 x 30 cm), placed in a 6 x 6 array, spaced approximately 25 m apart. Each trapping session consisted of 5 nights where

the traps were open, 2 nights with the traps closed and another 5 nights with traps open. Traps were checked twice daily, once in the morning and once in the evening and were covered in burlap for shade. All rabbits caught were sexed, weighed, and tagged (Monel no. 3, National Band and Tag, Newport, KY).

Radio-telemetry

Each rabbit weighing >1,000 grams was fitted with a radio-collar and a transmitter with an estimated 10-month operational life (Telonics, Inc., Mesa, AZ). Smaller rabbits (300-1,000 g) were fitted with a similar radio-collar, but with a velcro break-away device added to allow the animals to lose the equipment as their bodies grew larger. Collars were replaced as the animals aged.

Collared rabbits were located on separate days 3 times a week, once in the early morning (7-9 a.m.), once at mid-day (11 a.m. - 1 p.m.), and once in the evening (4-6 p.m.). Signals were followed until the animal could be seen or the exact location was found. All locations were made $\geq$24 hours apart to ensure independence of observations. Locations were plotted on 1:2400 aerial maps with 10-m^2 grid overlays. All road and water crossings were recorded and the distance of the water crossing was measured.

Home Range

All juvenile rabbits that were followed for more than 1 month (12 locations) were used for analysis of home ranges. The 12-location criterion was chosen because few juveniles were followed for more than 1 month. Attempts to determine a minimum number of locations for the adult home-range analysis by fitting the data to a negative exponential equation failed. None of the individuals had home-range sizes that reached an asymptote, despite the fact that some rabbits were followed their entire lives (Figures 4.1 and 4.2). Therefore, a minimum number of 30 locations (2.5 months) was chosen based on other studies of similar cottontail rabbits (Dixon and Chapman 1980; Kjolhaug and Woolf 1988). Computer program HOME RANGE (Ackerman et al. 1990) was used to determine sizes of minimum home ranges and to plot movements.

Because of the nature of Lower Keys topography and patterns of home ranges of marsh rabbits, several common methods of home-range estimation were excluded. The minimum convex polygon method (Hayne 1949) was rejected because it assumes that all areas within the perimeter of the outermost locations are used by the animal (White and Garrott 1990). Most of the marsh rabbits' home ranges contain unused areas, such as bodies of water, roads, or other man-made structures. One of the most statistically rigorous methods of calculating home-range size is the 95% probability ellipse (Jennrich and Turner

1969). It assumes that there is always only one center of activity (Harris et al. 1990), an assumption that was frequently violated in this study.

Two related methods that have worked well for analysis of rabbit home ranges are the harmonic-mean and core-area methods (Dixon and Chapman 1980). The harmonic mean is a nonparametric method based on a volume under a fitted 3-dimensional use distribution. It relates well to the actual distribution of locations. The core area (as calculated by program HOME RANGE), is the maximum area where the observed use distribution exceeds a uniform use distribution. Thus, it shows areas of particularly high home-range use and is relatively unaffected by outliers and sample size (Harris et al. 1990).

Seasonal differences in the home range size (95% harmonic mean and core area) were compared for each individual that was located at least 30 times in each season. The dry season locations occurred between November and April; the wet season was from May to October. Shifts in home range between season were also examined. Arithmetic centers of the dry and wet season home range of each individual were determined and the distance these centers shifted between seasons was calculated.

Spacing Behavior

The amount of overlap between the 95% harmonic mean and core areas of each individual was compared to other individuals living in the same habitat

patch. The first set of comparisons looked at all of the individuals of the same sex present at a patch during the same period of time. Percent overlap was determined by plotting all the home range contours together using Program HOME RANGE, and overlapping a 10 m grid. For each pair of individuals the amount of overlap was calculated as a percentage of the smaller home range.

This percent of overlap was compared to overlaps of same-sexed individuals living at the same patch but at different times, and pairs of opposite sexed individuals. A t-test was used for normally distributed data and when the variances between the 2 groups were equal. A Mann-Whitney U test was used when these conditions were not met.

Dispersal

If an animal appeared to be making a long-distance movement, it was located at least once every day. These locations were not used in any home range calculations. A rabbit that made a one-way long-distance movement was said to have dispersed. The criterion for dispersal as a movement was the diameter of the average marsh rabbit home range (Ribble 1992).

Dispersing animals were classified by sex and age class. Locations from the daily radio-telemetry session were plotted and straight lines were drawn between them to approximate the minimum distance traveled. Data on the demography of dispersers was used to test hypotheses on the cause of

dispersal. A hierarchical hypothesis design was used (Table 4.1) to attempt to narrow the potential cause of dispersal.

First, a binomial probability test was used to determine if the sex ratio of the dispersers was significantly different from unity. If this sex-ratio showed a significant bias, then trapping and radio-telemetry data were examined to determine if other adult males inhabited the disperser's natal patch. Trapping records of the adult males were further examined to determine if these males could potentially be the father of the dispersers. Potential fatherhood was assumed if the adult male was present at the disperser's natal patch around the time when the dispersers were believed to have been conceived.

Corridor Use

To determine if dispersing individuals were randomly leaving a patch or if they were influenced by potential corridors, paths of all individuals making one-way long distance movements were plotted. The proportion of each mover's trip (measured in meters) that covered different habitat types and the number of roads, runways, and bodies of water they crossed was measured. Table 4.2 lists the habitat types and features compared.

Using this distance as a radius with the arithmetic centerpoint of the natal home range as the center, a circle was drawn for each moving individual

(Figure 4.3). Aerial photographs were digitized (ARC/INFO 1990) to determine the amount of each habitat type and length of all roads, runways, and linear bodies of water was determined within this circle. The Johnson method (Johnson 1980) was used to determine if habitat use significantly deviated from the amount of each type of habitat available. A Waller-Duncan multiple comparison procedure (Waller and Duncan 1969) was used to determine differentially selected habitats. The Johnson method was chosen because it looked for overall differences in habitat use, not at individual habitat-use differences (Alldredge and Ratti 1992).

Results

A total of 54 Lower Keys marsh rabbits were caught and examined during this study. Forty-three were caught on the 6 main grid sites (41 on Boca Chica, 2 on Saddlebunch), 5 rabbits were caught while trying to recapture collared dispersed rabbits, and 6 were caught on other sites in the Lower Keys. Rabbits were only examined once per trapping period. Data from the 54 rabbits was recorded 130 times during eight trapping sessions (May 1991 - May 1993).

Forty-three (28 male, 15 female) of the rabbits caught were fitted with radio-collars, and 7 of these were juveniles. More juveniles were caught but at the time of their capture the break-away collars were not available. Forty-one

of the radio-collared rabbits were on Boca Chica Key and 2 were on Saddlebunch Key.

Home Range

Sufficient data were available for seven juveniles, 13 adult males, and 10 adult females for the home-range analysis (Table 4.3). Adult males were followed an average of >8 months (98 locations) and adult females were followed an average of >10 months (124 locations). Comparisons using the Wilcoxon test for differences between adult males and females did not show significant differences between the average distance moved between locations ($\underline{Z}$ = -1.71, $\underline{P}$ = 0.09), the 95% harmonic-mean home range ($\underline{Z}$ = -1.33, $\underline{P}$ = 0.18), or the core area ($\underline{Z}$ = -1.21, $\underline{P}$ =0.23). Resident adult males and females were similar with respect to their home-range shape and size (Figure 4.4). Both sexes appeared to establish a permanent home range shortly after maturity (9-10 months), and both resided in that area for the duration of their lives. Combining both sexes, the average 95% harmonic mean was 3.96 ha ($\underline{SE}$ = 0.65) and the average core area was 1.21 ha ($\underline{SE}$ = 0.87). Home-range size estimates for juvenile rabbits were not significantly different from adults, but 3 of the juveniles did not develop core areas. The lack of core area formation may be an attribute of juvenile home ranges or an artifact of the low number of locations used in the analysis.

There did not appear to be any significant changes in home-range size or shifts between the dry and wet seasons (Table 4.4, Figure 4.5). Results of a Mann-Whitney U test, used because the variances of the home range size were not equal, failed to find a significant result comparing either the wet and dry 95% harmonic home range ($T = 251$, $P = 0.45$) or core areas ($T=245.5$, $P =0.60$). None of the shifts in home range between the wet and dry seasons exceeded the radius the marsh rabbit's home range. However, ANOVAs testing the effect of time on home-range size were significant for both the 95% harmonic mean ($F = 6.25$, $df = 22$, $P = 0.02$) and the core area ($F = 5.55$, $df = 22$, $P = 0.03$). Animals increased their home-range size with time (and number of locations), irrespective of season.

Spacing Behavior

Figures 4.6 and 4.7 show the duration of each rabbit's radio-telemetry records and which rabbits were contemporaneous. The average amount of overlap between same-sexed individuals occupying a patch at the same time was significantly less than same-sexed groups occupying a site at different times (Table 4.5). This relationship held true using both the 95% harmonic mean home-range estimate ($t = -2.17$, $df = 12$, $P = 0.05$) and the core area ($t = -3.29$, $df = 12$, $P = 0.006$). When a rabbit died, same-sexed individuals living in adjent areas expanded their home ranges (Figure 4.8). Similarly, the

overlap between these contemporary same-sex individuals was significantly less than male/female overlap for both the 95% harmonic mean ($\underline{T} = 79.5$, $\underline{P} = 0.05$) and core area ($\underline{T} = 45$, $\underline{P} = 0.02$). In most cases there was little overlap between adults of the same sex (Figure 4.9).

Most males' home ranges overlapped 1 female at a time; 3 males overlapped 2 females simultaneously. During a portion of their lives, some males did not overlap with a female. Only 1 female overlapped with more than 1 male; this occurred for less than 1 month. Changes in overlap generally occurred when a rabbit died and another rabbit expanded his/her home range.

Home-range Features

All 43 rabbits, including the 7 juveniles, were used in the road- and water-crossing index. Only individuals that were currently in their natal or adult home ranges were used. Data from individual making long-distance movements were analyzed separately.

Home ranges of most of the marsh rabbits did not incorporate roads or large bodies of water. No water or road crossings were recorded for any of the juvenile rabbits. None of the rabbits crossed the major highway in the Keys (US-1). Only 1 adult female and 1 adult male crossed paved roads during the study. Rabbit A53F crossed a 2-lane several times. This same rabbit was the only adult female to cross a body of water; she regularly swam in shallow

water between mangrove prop roots while being radio-tracked. Male A51M also crossed a 2-lane road four times. Neither rabbit crossed the road to visit another "patch". Female A53F crossed the road to swim in the water adjacent to her home "patch"; male A51M crossed the road when construction was being completed in the corner of his home patch.

Dispersal

Seventeen rabbits (11 male, 6 female, all subadults) made permanent one-way movements (Table 4.6). The minimum dispersal distance was calculated using the diameter of the combined adult core-area size. Assuming a circular home-range shape, the average diameter was 124 m.

Eleven of the subadults made movements >124 m. Ten of the dispersers were male and one was female. Only 1 of the males failed to meet the criterion for dispersal, and whereas 5 of the females did not exceed the distance. In general, the males made long-distance movements far in excess of the criterion, including a 3-day movement that placed a male over 2 km from his natal range. Most of the females settled near their natal ranges, including the female that was classified as a disperser.

The sex ratio of the dispersers was significantly male biased (binomial $P < 0.001$). Six of the males that dispersed left patches where there was another adult male present, but 4 left patches where there were no adult males. Five of

the males that dispersed left patches were the male present could have been their father, but the other 5 left patches were there either were no males present, or a male too young to be their parent was present. The 1 subadult male that did not disperse occupied a patch where there were no other adult males.

Corridor Use

Subadult rabbits traveled through a variety of habitats between their natal and permanent home ranges. Three rabbits crossed a dirt road, 7 crossed a 2-lane road and 3 rabbits were observed crossing taxiways and runways. None of the rabbits crossed the 4-lane highway (US 1), but none of the dispersal radii encompassed or were adjacent to the highway. Two rabbits swam across ditches, 1 across a canal, and 1 crossed a (12 m) body of water.

In general, most of the subadult rabbits traveled through areas with dense ground cover. These marsh rabbits were recorded traveling through mangroves, upland hardwood hammocks, and in the vegetation between the shoulder of the road and the water. The narrowest strip of plant cover used (corridor) by a dispersing marsh rabbit was 3-5 m wide. The Johnson test that compared the amount of each habitat traveled through compared to its use was significant ($F = 6.62$, $df = 3,14$, $P = 0.005$). A Waller-Duncan comparison found that rabbits used areas of mangrove, hardwood hammock, and transition

zone significantly more than expected and used disturbed areas significantly less.

Discussion

The data suggest that members of S. p. hefneri spend most of their lives in 1 patch, but can move to other patches. Marsh rabbits are born in a patch of transition-zone habitat and remain there until they reach sexual maturity. At sexual maturity most rabbits make a relatively long, one-way movement. Male marsh rabbits may move a great distance away from their natal range; females are more likely to remain in the same patches where they were born. If a patch is relatively small, this movement may mean leaving the habitat patch. When these subadult marsh rabbits leave their natal ranges, they establish adult home ranges that they maintain for their lifetime. These adult home ranges do not incorporate any roads (2-lane and larger) bodies of water, or other types of habitat. All mating appears to occur within the same habitat patch. These results are consistent with the predictions of the second hypothesis, that S. p. hefneri exists in a metapopulation (Levins 1970, Hanski 1991).

The Lower Keys marsh rabbit's ability to exist as a metapopulation and disperse over relatively long distances may be a product of inhabiting a naturally patchy environment (Opdam 1991, Thomas 1994). Species that exist in temporally or spatially patchy environments must be able to deal with

isolation at a more regional scale than those species that occupy more permanent, interconnected habitats. Marsh rabbits throughout their range occupy upper marshes along the coasts and interior wetlands, much of which is patchily distributed. Before European colonization in the Keys, the transition zone was probably more contiguous. Most of the habitat types in the Keys exist in contiguous, concentric rings; habitat type is largely determined by elevation.

Spatial Organization

Marsh rabbit home-range size was well within the range for cottontail species (Chapman et al. 1982). The 95% harmonic mean estimates represent a conservative estimate of the amount of habitat used; the core area estimate delineated the area needed for more intense use. Despite strong seasonally of the rainfall in the Keys, home ranges were consistent throughout the year.

Similar to the eastern cottontail and the swamp rabbit, there is little overlap in home ranges of members of the same sex. Marsh rabbits may be territorial within their sex. Most current definitions of territoriality specify that an area must be used exclusively (at least within the sex) and that it must be actively defended (Eisenberg 1981, Begon et al. 1990). To be truly territorial, marsh rabbits would have to defend their home ranges. Territorial defense is difficult to observe in the field, especially in a secretive, crepuscular species

like the marsh rabbit. Some circumstantial evidence of physical defense was apparent in the males; 76% of the subadult and adult males had scratch marks and scars on their face, ears and back of their heads. Boxing, scratching, and paw-raking with the feet has been observed in other species of cottontails (Marsden and Holler 1964) and may be responsible for the scratch marks. Generally these behaviors are related to competition for mates (Eisenberg 1981). Female marsh rabbits showed no signs of scratch marks. It is not readily apparent why it would be advantageous for the females to be territorial, however there is some evidence that nesting sites may be limited (see Natality - chapter 3). Fecal pellet marking is well-developed in other rabbit species (Teft and Chapman 1987) and may be used by male and female marsh rabbits to mark the boundaries of their home ranges.

Both males and females increased their home ranges following the death of a conspecific. Over the lifetime of a rabbit this was seen as an increase in home range with age. This phenomenon provides additional support that some spacing behavior is partially determining home-range size. This spacing behavior may have an impact on population density and total abundance of rabbits in a habitat patch.

Most of these home ranges consisted almost exclusively of transition-zone habitat. Physical features such as canals, roads, and runways were rarely crossed by any of the adult marsh rabbits, despite the proximity of the features.

The definition of a habitat patch put forth in the methods section appears to be valid.

Subadult marsh rabbits were more likely to cross these barriers and use alternate types of habitat. However, their movements did appear to be influenced by the surrounding habitat matrix. Concordant with other studies on rabbit movements (Chapman 1971, Trent and Rongstad 1974), marsh rabbits were more likely to cross the more densely vegetated native habitats (transition zone, hardwood hammock, and mangrove) than the more open, disturbed areas. Presence of these habitats around the natal patch appeared to facilitate movement between patches of transition zone habitat, acting as corridors in the highly fragmented landscape (Wilson and Willis 1975). These results support the patch geometry models (Buechner 1987, Stamps et al. 1987) rather than the random walk theory (Berg 1983).

Dispersal has not been well studied in other species of cottontails. Results from the telemetry indicate that most long-distance dispersers were young males, similar to most polygynous mammalian species (Dobson 1982). The small patch size and low density of rabbits in this study provided a unique opportunity to investigate the cause of dispersal. Because some of the males dispersed despite the lack of other adult males at their natal patch, the competition-for-mates hypothesis cannot entirely explain all of the movements. Similarly, lack of potential fathers at most of the natal patches excludes the

resident fitness hypothesis as being the sole explanation. Only the inbreeding avoidance hypothesis is consistent with all of the data collected. It is possible that dispersal may be motivated by several factors (Dobson and Jones 1985) and that there may be variance between individuals. This interpretation is based only on current dispersal patterns. Current dispersal behavior may be a response to population structure in evolutionary time. The marsh rabbit population structure has probably undergone dramatic changes since the colonization of man in the Keys.

Conclusions

These results imply that the S. p. hefneri should be managed as a metapopulation. Each local population is socially isolated from the other populations. Interchange generally occurs by movement of subadult males and this movement is facilitated by the occurrence of habitat corridors. The impact these conclusions has on the persistence of S. p. hefneri will be addressed in chapter 6.

Table 4.1--Hierarchical tests and predictions of the proximate cause of dispersal.

Prediction	Cause of Dispersal
I. An equal number of males and females disperse	Competition for resources
II. Only one sex disperses.	
A. The dispersers are all female.	Inbreeding avoidance
B. The dispersers are all male.	
1. A male disperses only if another adult male is present at the habitat patch.	Competition for mates
2. A male disperses only if other males are present and could potentially be their father.	Resident fitness hypothesis
3. All males disperse regardless of the presence or absence of other males.	Inbreeding avoidance

Table 4.2--Habitat types and possible physical barriers encompassed by Lower Keys marsh rabbit (Sylvilagus palustris hefneri) dispersal movements.

Feature	Mode of measurement
Unimproved road (dirt, gravel)	meters of length
2-land road	meters of length
4-land highway	meters of length
Mosquito drainage ditch (water < 1m)	meters of length
Canal (1 - 10 m)	meters of length
Major body of water (water > 10m)	meters of length
Disturbed or barren habitat	ha
Mangrove	ha
Hardwood hammock	ha
Pineland	ha

Table 4.3--Home-range data on Lower Keys marsh rabbits (Sylvilagus palustris hefneri) observed for >1 month for juveniles, >30 locations for adults.

Rabbit	Classification	Number of locations	Distance between consecutive locations (m)	95% harmonic mean home range (ha)	Core area (ha)
J55M	Juvenile	30	69.58	13.83	4.44
J99M	Juvenile	18	47.40	2.49	0.64
J101F	Juvenile	16	22.99	0.10	
J102F	Juvenile	21	25.81	1.11	0.38
J103M	Juvenile	14	22.39	0.30	
J199M	Juvenile	14	40.60	0.81	
		x	38.13	3.11	1.82
		SE	(7.55)	(2.17)	(1.31)
A51M	Adult male	122	48.34	11.94	3.15
A55M	Adult male	70	30.81	2.73	0.89
A59M	Adult male	79	28.71	2.13	0.93
A63M	Adult male	217	25.33	5.81	1.58
A64M	Adult male	61	17.87	0.36	0.02
A67M	Adult male	99	42.10	3.47	1.10
A68M	Adult male	142	35.30	3.63	1.24
A69M	Adult male	138	50.88	7.61	2.60
A70M	Adult male	88	36.85	2.99	0.86
A71M	Adult male	67	37.47	3.18	1.22
A73M	Adult male	60	38.24	4.23	1.20
A75M	Adult male	74	28.07	4.35	1.18
A85M	Adult male	54	52.36	2.81	1.03
		x	36.33	4.25	1.31
		SE	(2.85)	(0.80)	(0.22)
A50F	Adult female	252	28.14	6.52	2.00
A52F	Adult female	127	34.31	10.32	3.17
A53F	Adult female	201	59.76	8.60	2.09
A57F	Adult female	220	21.90	1.67	0.53
A58F	Adult female	90	20.90	0.72	0.24
A72F	Adult female	107	26.15	2.49	1.02
A74F	Adult female	75	27.89	1.27	0.46
A76F	Adult female	81	22.12	1.53	0.53
A86F	Adult female	44	32.68	1.72	0.53
A176F	Adult female	45	30.52	0.98	0.25
		x	30.44	3.58	1.08
		SE	(3.56)	(1.12)	(0.32)

Table 4.4--A comparison between the wet and dry season home ranges (ha.) of Lower Keys marsh rabbits (Sylvilagus palustris hefneri). The distance between the centers of each home range is compared to the radius of the 95% harmonic mean and core area estimates.

ID	Wet season			Dry season						
	#locals	95% harmonic mean	Core area	#locals	95% harmonic mean	Core area	95% harmonic radius	Core radius	Meters moved	Core radius - meters moved
A70M	36	0.81	0.24	52	2.79	0.83	50.79	27.65	15.52	12.13
A71M	36	2.99	0.90	31	1.31	0.54	97.58	53.54	24.50	29.04
A68M	64	3.79	0.90	78	1.37	0.47	109.86	53.54	38.11	15.43
A67M	45	4.03	0.96	54	0.56	0.14	113.29	55.29	37.00	18.29
A63M	124	2.28	0.57	93	5.74	1.60	85.21	42.61	14.14	28.47
A69M	60	6.31	2.04	78	3.61	1.42	141.76	80.60	13.01	67.59
A59M	43	1.95	0.87	36	1.48	0.46	78.80	52.64	45.45	7.19
A55M	36	2.16	0.80	34	0.91	0.40	82.94	50.48	24.02	26.46
A51M	73	0.53	0.33	49	0.45	0.28	41.08	32.42	5.00	27.42
A72F	36	1.15	0.37	71	3.26	1.23	60.52	34.33	39.11	-4.78
A53F	81	10.18	2.51	120	6.50	1.72	180.06	89.41	45.17	44.24
A50F	132	3.49	1.04	120	5.60	1.75	105.43	57.55	12.17	45.38
A58F	48	1.46	0.47	42	0.43	0.20	68.19	38.69	28.07	10.62
A57F	106	1.38	0.45	114	0.78	0.27	66.29	37.86	9.84	28.02
A52F	78	6.21	2.21	49	7.15	2.31	140.63	83.89	4.24	79.65

Table 4.5--The amount of overlap between same and opposite sexed individuals occuping a site during the same time and between same-sexed individuals that occupied the same site during different times.

Same sex-same time			Same sex-different time			Opposite sex-same time		
Pair	95%	Core area	Pair	95% har.	Core area	Pair	95% har.	Core area
A59M/A55M	34%	12%	A51M/A69M	100%	43%	A51M/A52F	100%	67%
A63M/A67M	30%	3%	A55M/A75M	82%	44%	A59M/A57F	68%	40%
A70M/A71M	85%	42%	A59M/A55M	45%	20%	A59M/A58F	45%	22%
A50F/A74F	9%	2%	A59M/A75M	91%	72%	A60M/A53F	44%	22%
A53F/A76F	100%	21%	A53F/A76F	100%	100%	A63M/A50F	54%	32%
A57F/A58F	16%	0%	A57F/A86F	71%	74%	A64M/A53F	8%	0%
A72F/A65F	0%	0%	A58F/A86F	45%	20%	A67M/A50F	100%	100%
						A67M/A74F	85%	21%
						A68M/A76F	100%	90%
						A70M/A65F	8%	2%
						A70M/A72F	82%	48%
						A71M/A72F	90%	84%
						A75M/A57F	100%	100%
						A75M/A86F	100%	86%
Average	39%	11%		76%	53%		70%	51%

Table 4.6--Data on radio-collared marsh rabbits that made permanent, one-way movements. Rabbits were caught on Boca Chica, Geiger, and Saddlebunch Keys between June 1991 to May 1993.

Rabbit	Classification	Distance between natal site and last location (m)	Body mass at beginning of movment (g)
A48M	Subadult male	550	1,000
A49M	Subadult male	550	1,050
A54M	Subadult male	920	1,050
A55M	Subadult male	1,100	800
A56M	Subadult male	1,800	1,000
A60M	Subadult male	510	1,000
A66M	Subadult male	60	800
A68M	Subaudlt male	180	1,000
A69M	Subadult male	980	800
A84M	Subadult male	2,050	1,050
A197M	Subadult male	400	900
$\bar{x}$		827	950
SE		191	32
A3F	Subadult female	60	850
A65F	Subadult female	40	900
A74F	Subadult female	70	950
A76F	Subadult female	80	900
A86F	Subadult female	90	1,000
A176F	Subadult female	150	900
$\bar{x}$		82	917
SE		15	21

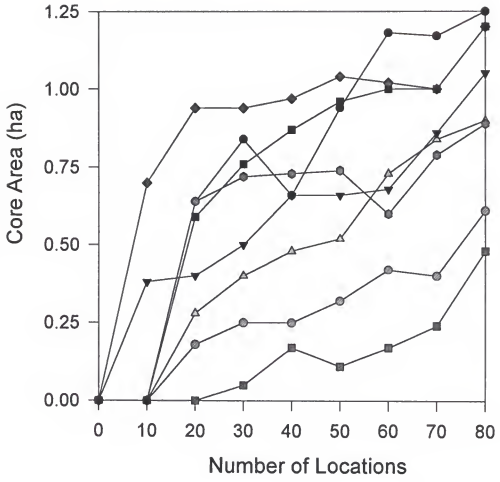


Figure 4.1--The cumulative core area measurements of 8 radio-collared male Lower Keys marsh rabbits (Sylvilagus palustris hefneri).

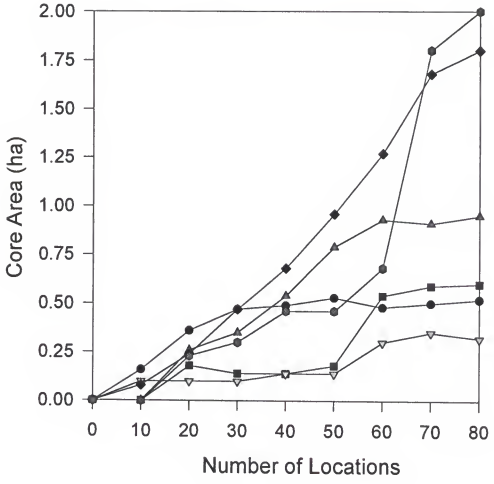


Figure 4.2--The cumulative core area measurements of 6 radio-collared female Lower Keys marsh rabbits (Sylvilagus palustris hefneri).

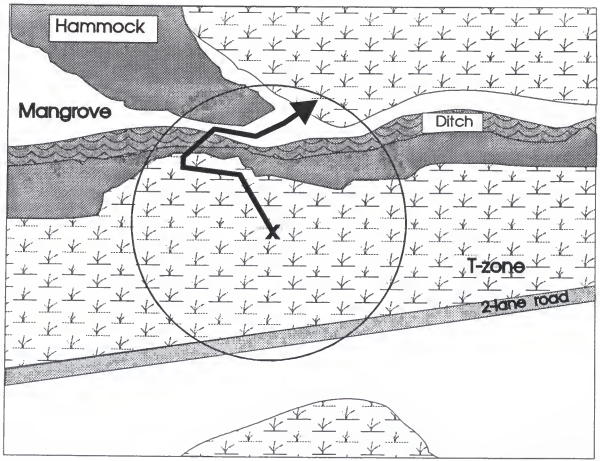


Figure 4.3--To determine if a dispersing Lower Keys marsh rabbit (Sylvilagus palustris hefneri) used certain habitat as a corridor, the habitat type the rabbit moved through was compared to the habitat available. Using the centerpoint of the rabbit's natal home range and the distance dispersed as a radius, a circle of available habitat was drawn. The arrow indicates the actual patch the rabbit took.

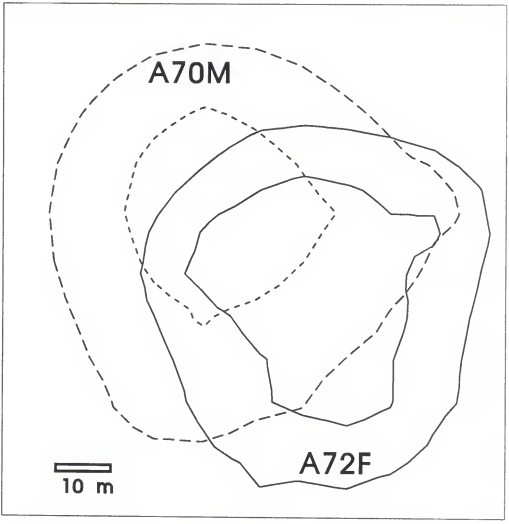


Figure 4.4--Home ranges using the 95% harmonic mean (outer boundary) and core areas (inner boundary) of a sympatric male and female Lower Keys marsh rabbit (Sylvilagus palustris hefneri) at site #7 on Boca Chica Key.

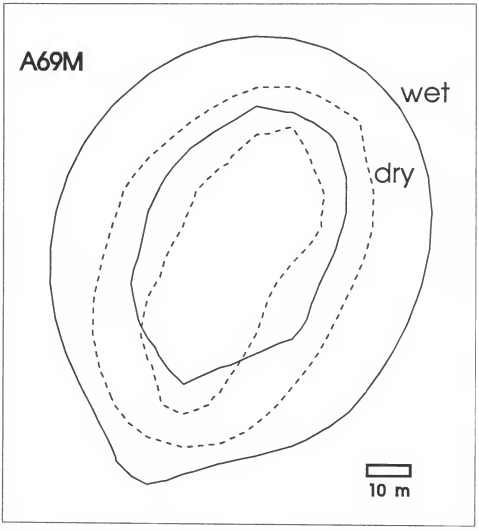


Figure 4.5--A comparison of the wet and dry season home ranges using the 95% harmonic mean (outer boundary) and the core area (inner boundary) for an adult male at site 10.

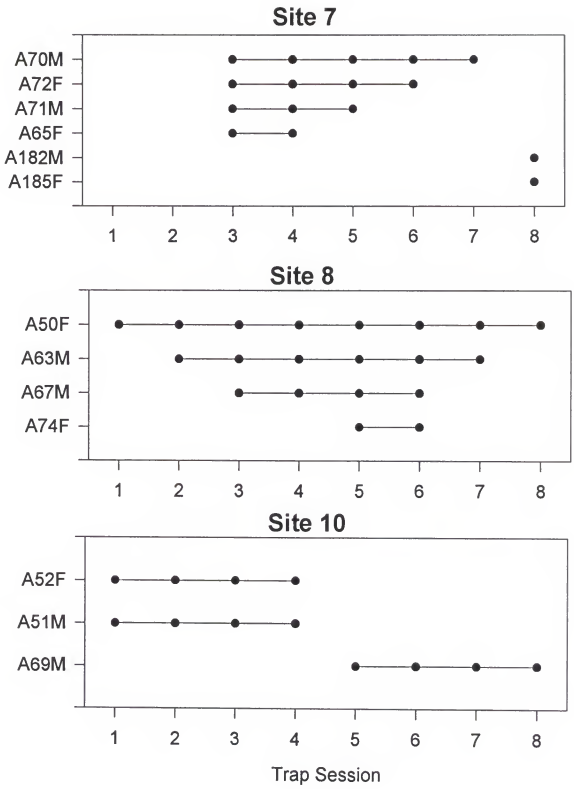


Figure 4.6--The duration that radio-collared Lower Keys marsh rabbits (Sylvilagus palustris herneri) were followed at sites #7, #8, and #10.

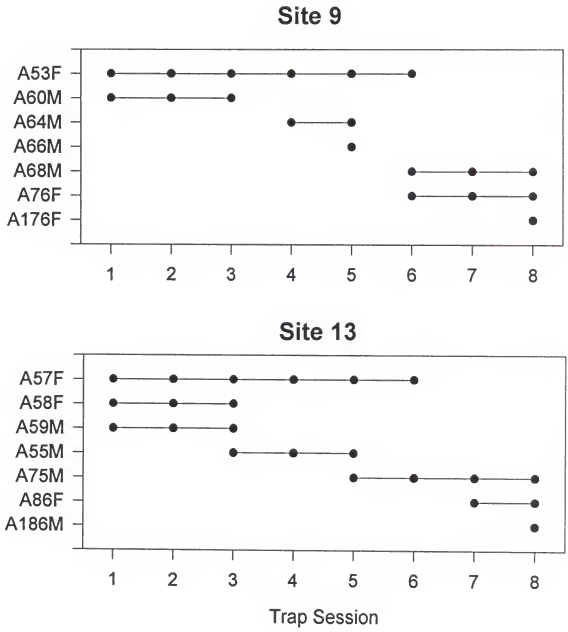


Figure 4.7-- The duration that radio-collared Lower Keys marsh rabbits (Sylvilagus palustris herneri) were followed at sites #9 and #13.

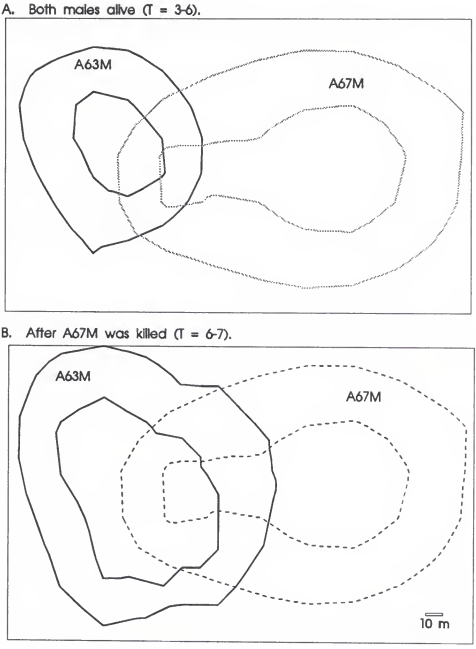


Figure 4.8--The home ranges using core area, of 2 sympatric males telemetered between session 3 and 6 (A.) and the expansion of A63M's core area after the death of A67M.

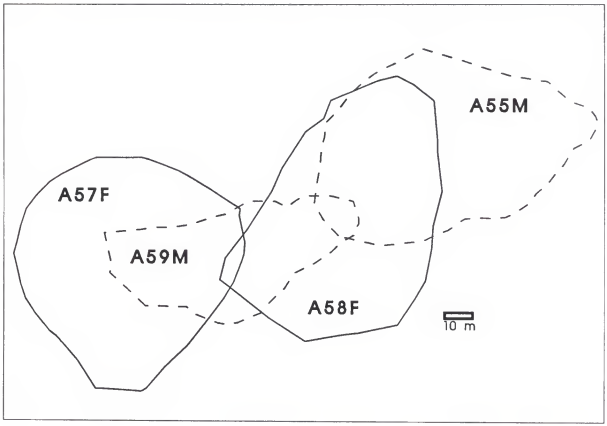


Figure 4.9--The core areas of 4 sympatric Lower Keys marsh rabbits (Sylvilagus palustris hefneri). Rabbit's A55M and A59M are adult males, A57F and A58F are adult females.

CHAPTER 5
METAPOPULATION DYNAMICS: PATCH OCCUPANCY AND HABITAT QUALITY

Introduction

In Levins' (1969) metapopulation model, all habitat patches were identical in size and quality. More recent models (Taylor 1991, Thomas et al. 1992, Hanski 1994, Hanski et al. 1994), have taken an incidence-function approach (Diamond 1975) that predicts the probability of a species' occurrence based on the area of the habitat and the distance of the habitat patch to other patches. In these models, all patches are assumed to be inhabitable past a threshold size or minimum isolation (Hanski 1994). For species whose natural history is relatively unknown, an important aspect of a metapopulation occupancy model is determining if unoccupied habitats are vacant due to lack of suitable habitat or from past extinctions unrelated to the habitat patch quality.

Metapopulation Structure

Before studying habitat use, metapopulation structure should be studied to determine how the subpopulations interact with each other. In a "classical

metapopulation" all patches greater than a minimum area and less than a maximum isolation are suitable for supporting a population. Local extinctions (due to deterministic or stochastic causes) are counteracted by colonizations from near-by patches (Hanski and Gilpin 1991). Some classic metapopulations may resemble the stepping-stone model of occupancy (Gilpin 1980). In this model, the probability of occupancy increases as patch size increases and distance to the nearest occupied patch decreases as a dynamic consequence of local extinction and colonization.

In a "mainland-island" metapopulation, 1 or a few large patches are occupied continuously while surrounding small patches frequently experience extinction but are recolonized due to their proximity to a mainland patch (Harrison 1991, 1994). Only patch size determines which patches will be mainlands and which patches are islands. Larger patches (and hence larger populations) are able to maintain occupancy despite population variability and thereby act as mainlands from which individuals emigrate to the smaller islands.

Although similar to mainland-island metapopulations, source-sink metapopulations differ because habitat quality explains the patterns of occurrence. In a source-sink metapopulation the higher quality source habitat patch produces a surplus of descendants ($\lambda > 1$) whereas the low-quality patches may be sinks that produce a deficit ($\lambda < 1$) (Pulliam 1988, Pulliam and

Danielson 1991). Individuals from source populations migrate to sink populations, giving the false appearance that these sink habitats are suitable for the species. Habitat sources and sinks should be analyzed separately for information on habitat requirements.

Habitat Use

An animal selects a habitat based on proximate cues from the environment, but the decision will ultimately affect the individual's fitness in terms of survival and reproduction (Lack 1933, Levins 1969, Cody 1985). For many species, habitat selection is difficult to determine and habitat use is the best available information. Assessment of habitat use is based on correlation of the actual distribution of individuals with specific habitat features. It may be inferred that habitat use is the outcome of habitat selection (Bergin 1992).

Habitat use may be studied at several spatial and temporal scales. For a small-to-medium sized herbivore, the smallest scale may involve the leaf browsed (diet). At the next level habitat use includes the areas used for foraging and nesting within a habitat patch (microhabitat). At the largest scales, the features that influence the presence or absence of a species over time at a particular habitat may be studied (macrohabitat).

The first objective of this chapter is to determine the relationship among habitat patches within the Lower Keys marsh rabbit metapopulation. The

spatial arrangement, size of the patches, and patterns of occupancy will be examined to determine if the metapopulation is classical, mainland-island, or source-sink in structure.

The second objective of this chapter is to elucidate factors influencing habitat use by the Lower Keys marsh rabbit at 3 inter-dependent spatio-temporal scales. This habitat analysis will be used to determine if currently unoccupied habitat patches are suitable and empty because of their isolation from other patches or if the habitat is unsuitable.

Methods

Fecal pellets were used to study diet, habitat use, and the presence/ absence of marsh rabbits. Presence of fecal pellets can be an accurate and efficient method of studying habitat use and patch occupancy when information about pellet persistence is estimated (Simonetti and Fuentes 1982, Pietz and Tester 1983). It is a particularly useful method for species that are secretive, crepuscular, at low densities, and not easily trappable (Wood 1988).

Pellet Grids

Permanent fecal pellet-sampling grids were established at each of 59 patches of transition-zone habitat in the Lower Keys. The grid was designed to fit into the smallest patch and consisted of a square of 7 x 7 stations at 15-m

intervals, marked with permanent flags. The grids were surveyed 3 times per year: March (late dry season), July (mid-wet season) and November (transition between wet and dry) from March 1991 to July 1993. Each survey consisted of a pellet removal within a radius of 0.5 m at each station followed by a pellet census 1 month later (a marker had pellets if 1 pellet fell within 0.5 m). A grid was considered to be occupied (marsh rabbit present) if at least 1 of the stations had a marsh rabbit pellet.

To ensure that fecal pellets did not begin to degrade in less than a month, during each survey 100 of the pellets from captured rabbits were placed on a transition-zone grid. The pellets were separated into 4 groups and placed on rocks, on mud, in grass, and under trees. The pellets were counted weekly to determine the rate of decomposition.

Pellet Size

To determine if the pellets produced on a grid were from juvenile or adult marsh rabbits, a linear regression was used to determine if body mass accurately determines pellet size. Body mass was obtained by trapping individual marsh rabbits at 6 sites in the Lower Keys, including the 5 main sites on Boca Chica (Figure 3.1) and 1 site on Saddlebunch. Trapping occurred twice during the wet season (June - November), and twice during the dry season (December - May). For the 5 sites on Boca Chica Key, trapping

occurred from June 1991 to May 1993 (8 trapping sessions). On Saddlebunch, trapping was conducted from June 1992 to May 1993 (4 trapping sessions). Trapping grids were placed on each site, using unbaited collapsible National live traps (80 x 30 x 30 cm), placed in a 6 x 6 array, spaced approximately 25 m apart. Each trapping session consisted of 5 nights where the traps were open, 2 nights with the traps closed and another 5 nights with traps open. Traps were checked twice daily, once in the morning and once in the evening and were covered in burlap for shade.

All rabbits caught were sexed, weighed, and tagged (Monel no. 3, National Band and Tag, Newport, KY). For the purposes of this part of the study, adult marsh rabbits were those that weighed >1000 g, smaller rabbits were classified as juveniles. Ten fecal pellets were collected in a pan underneath each trap and the width and length of each pellet was recorded. The average area (width x length) was used in the regression. Each rabbit was used only once in the analysis.

Metapopulation Structure

Sites were classified based on site occupancy; if a site was never occupied during the past 2 years it was classified as being "empty", if it was occupied at least once it was called "variable" and if it was consistently occupied it was referred to as an "occupied" site. Sites were graphed using the

common log of area and isolation (distance to nearest occupied patch), and the result was compared to theoretical patterns for classic, mainland-island and source-sink (Figure 5.1).

Occupied and variable patches were further compared to determine if they were sources and sinks. Liberal definitions of source and sink were used; a source was any patch where reproduction occurred when occupied, and a sink was any patch where only adult rabbits were present. Presence of adults and juveniles was determined by measuring the size of the pellets found on the grid. Because it was previously determined (in Chapter 4) that juveniles remain in their natal patch until they become subadults, it was assumed that at least 1 juvenile pellet present on the grid indicated presence of reproduction occurring on that grid. For each habitat patch the number of surveys where juvenile pellets were found was compared to the number of surveys occupied.

Dietary Analysis

Pellets for dietary analysis were collected from the pans beneath the rabbit traps from the 5 sites on Boca Chica. To avoid experimental bias, pellets were collected only from adult animals 1 time. At each of the 5 Boca Chica sites, pellet samples were collected from eight rabbits, 2 from each sex during both the wet and dry seasons, totaling 40 pellet-group samples.

Fecal pellets were dried and crumbled to prepare microscope slides following standard procedures (Johnson et al. 1983). One hundred microscope fields (20/slide) were examined for each sample. Plant species were identified by comparing epidermal structures from the samples with a reference collection of plant tissues collected in the area. Average relative densities were calculated for each food item per pellet-group sample.

Relative densities of vegetation in the pellets may not be directly comparable to the amount of each vegetation ingested. Variation in the digestion and retention rate of each type of vegetation can bias the results (Wallage-Drees et al. 1986, Westoby et al. 1976, Batzli and Pitelka 1971). These biases can be quantified by comparison of fecal and stomach samples, but this is impractical in many studies (Johnson and Pearson 1981), especially those involving endangered species.

To avoid these problems, and still obtain data on the differences between available vegetation and vegetation in the rabbit's diet, we compared the species available and the species used. We assumed that although different types of vegetation vary in their digestibility, most vegetations would still be present in the fecal pellet sample if they had been ingested. Available vegetation (ground cover <1.5 m) at the 5 sites was estimated using the line intercept method (Canfield 1941). Ten 5-m long transects were randomly

located at each site and percent occlusion was determined for each plant species.

The relative densities are comparable between samples, because the digestion and retention rates are fairly constant for each plant species (Wallage-Drees et al. 1986). Univariate analyses of variance (PROC GLM, SAS Institute, Inc. 1988) were performed on arcsine-transformed estimates of dietary composition (%) for the most abundant species in the samples. Data from the 2 years were pooled to provide sufficient sample sizes to examine the differences between pellet groups from different sites, seasons, and sexes.

Microhabitat Use

Microhabitat use was studied at each of the most accessible sites (sites that were not high securtity) on Boca Chica Key (sites 1 -17, Appendix A). Detailed data were recorded on vegetation at each of the 49 permanent markers (49 quadrats) on the 17 grids. Based on species composition, each site was classified as being in 1 of 4 habitat categories: low marsh (dominated by Monanthocloe littoralis, Sesuvium maritimum, Salicornia virginica, Batis maritima, and some small mangrove trees), mid-marsh (dominated by Borrichia sp. and Sporobolus virginicus), high marsh (predominantly the clump grasses Spartina spartinae, and Fimbrystylis sp.), and hammock (dominated by tree species, mainly Conocarpus erectus). Four categories is an adequate number of

habitat groups suggested by Alldredge and Ratti (1986) for controlling Type II statistical errors.

Presence or absence of pellets was recorded at each marker during March, July, and November (from November 1991 - July 1993). A Chi-square Goodness-of-fit test was used to determine whether there was a significant difference between the "expected" use of habitat classes (the proportion of quadrats in each habitat category) and the observed frequency of habitat usage (the proportion of quadrats with pellets). If a statistically significant overall result was found, habitat selection was determined by using Bonferroni confidence intervals (Neu et al. 1974, Byers and Steinhorst 1984).

Macrohabitat

Macrohabitat variables were measured at each of the 59 sites in the Lower Keys (Appendix A). The variables included the traditional metapopulation geometric variables, area and isolation. In addition, at each grid vegetation characteristics were measured using a line intercept method (Canfield 1941). Ten 5-m long transects were randomly located at each site and percent occlusion was determined for each plant species. Two vegetation layers were used: ground vegetation of plants <1.5 m in height and canopy vegetation of plants ≥1.5 m. Ground cover, canopy cover, average maximum ground vegetation height, and plant diversity were calculated from these

transects. The Shannon-Weaver diversity index (H') was chosen because species composition and abundance were taken from transect data (Shannon and Weaver 1949). In addition, the percent cover of individual species found to be important to marsh rabbit diet and microhabitat were also included. Results from the most recent vegetation survey (July 1993) were used in the analysis. Landscape characteristics (area, distances to water, occupied domiciles, and other marsh rabbit populations) were measured from USGS topographic maps (1:24,000).

Variables were screened for normality and significant inter-correlation before analysis. Non-normal variables were subjected to logarithmic and square-root transformations. If a significant correlation was found between variables, the variable with the most meaningful biological interpretation was retained.

Two DFAs were performed on the data. The first compared the empty sites to those that were occupied by rabbits during some portion of the study (variable and consistently occupied sites). The second DFA compared variable sites to the consistently occupied sites. Results of the second discriminant function were used to reclassify the empty sites, to determine (based on habitat features alone) if they are suitable for marsh rabbit recolonization. It was assumed that if reintroduction was to occur, rabbits would be released at

several sites on 1 key. The distance to the nearest occupied patch was calculated using this assumption.

Statistical analyses were done using procedures STEPDISC and DISCRIM (SAS Institute, Inc. 1985). First, a stepwise discriminant function analysis was used to select a subset of variables that produced a good discrimination model. A value of $\underline{P} < 0.15$ was used a criterion for model inclusion. These variables were then entered to determine a discriminant function for site classification. The model was validated using a jackknife procedure (Capen et al. 1986). The jackknife procedure classifies each sample using the discriminate equation derived form all samples except the 1 currently being classified (Lachenbruch 1975).

Results

Pellet Degradation Rate and Pellet Size

During the first survey, pellets began to disappear off the grid after 7 weeks (Figure 5.2), indicating that during the dry season any sampling period less than 7 weeks should suffice for density estimation based on pellet counts. To compensate for a reduced persistence time anticipated for the wet season, a sampling period of 1 month (T = 30 days) was chosen for pellet accumulation before making counts. During the following 7 surveys, this duration was found to be adequate for all seasons. In each session, pellets under trees in the litter

took the longest time to decay, whereas those in mud decayed in the shortest time.

Fifty-three rabbits (19 females and 34 males) each produced 10 intact pellets and were included in the regression of body mass and pellet area. The relationship was strong and significant for both males ($F = 95.8$, $P < 0.0001$, $r^2 = 0.75$) and females ($F = 198.6$, $P < 0.0001$, $r^2 = 0.92$). The regression lines were very similar, and both regression equations produced a pellet area of 0.4 cm^2 for a body mass of 1000 g (Figure 5.3). This pellet area was used to distinguish between adult and juvenile pellets on the pellet grids. It was determined in Chapter 3 (Growth and Morphology) that most rabbits were sexually mature by 1000 g and considered to be adults.

Metapopulation Structure

Marsh rabbits were found at sites on Boca Chica, Saddlebunch, Sugarloaf, and Big Pine Keys (Figure 5.4). Between Sugarloaf and Big Pine Key, a gap in the distribution of marsh rabbit populations occured, despite the presence of transition-zone habitat.

Of the 59 patches of transition zone habitat used in the analysis (Figure 5.5), 20 had pellets present during all of the surveys (occupied patches), 22 had pellets present during at least 1 survey (variable patches), and 17 never had any pellets present (empty). When these patches were plotted by log area and

isolation (Figure 5.6), area did not have a large effect on whether a patch had rabbits present (variable or occupied). There did appear to be a maximum isolation (inter-patch distance) beyond which no rabbits occurred on patches. This maximum isolation occurred around 2000 m (2 km) and is similar to the maximum dispersal distance for males (Figure 5.7).

When the metapopulation structure of the S. p. hefneri was compared to the predicted structures (Figure 5.1), it appeared that it did not fit 1 pattern perfectly. The structure was most similar to the classical metapopulation structure. An examination of patch extinction and recolonization on Big Pine (Figure 5.8) demonstrates that patches of all sizes went extinct during the study and were often recolonized. Of the 22 sites that had had pellets present for at least 1 but not all of the surveys, 11 were observed to go extinct during the study. Four of those local extinctions were recolonized.

The Lower Keys marsh rabbit metapopulation was least similar to the mainland-island structure. In the mainland-island pattern, only large patches are permanently occupied; yet in the observed pattern, patches of all size appeared to be permanently occupied and some of the largest sites were variably occupied.

In the source-sink model, low-quality patches that are near source patches are often variably occupied, while low-quality patches that are further away are empty. This appeared to be partially true in the marsh rabbit

metapopulation structure, yet some of the small, nearby patches were permanently occupied as might be seen in a classic metapopulation.

Consistently occupied patches had juvenile pellets present for significantly more sessions than variably occupied patches ($t = -2.67$, $P < 0.01$). The average proportion of sessions with juveniles was 54.2% (SD = 26.1) for the consistently occupied sites and 29.9% (SD 26.05) for the variably occupied. Six of variably occupied sites and only 1 of the consistently occupied sites never had juvenile pellets present. The variable sites could produce juveniles, but they were less likely to than the consistent patches. Further analysis of differences in habitat quality was warranted.

Dietary Analysis

Nineteen plant species representing 14 families were found in the fecal pellets of 40 rabbits (Table 5.1). Two grasses, Sporobolus virginicus and Spartina spartinae, composed over 50% of all diets. Sporobolus virginicus occurs predominantly in the low marsh while S. spartinae dominates the high marsh. Two mangrove species, Laguncularia racemosa and Rhizophora mangle, and a small succulent shrub Borrichia frutescens, made up another 25%. The remainder of the species were grasses, sedges, shrubs, and trees.

Three species, Monanthochloe littoralis, Conocarpus erecta, and Pithecellobium guadelupense, were abundant at the transition-zone sites but

absent from the marsh rabbit's diet (Table 5.2). Key grass (M. littoralis) is a short wiry grass, and buttonwood (C. erecta) and blackbead (P. guadelupense) are tree species. Excluding these species, marsh rabbits generally fed on the most abundant species available.

The 4 most abundant species in the fecal pellets, S. virginicus, S. spartinae, B. frutescens, and L. racemosa, were used in the univariate analysis. Univariate analysis indicated a significant between-season difference in the relative density of S. spartinae in the fecal pellets, and a significant season-by-sex interactions in presence of S. virginicus and of S. spartinae (Table 5.3). There were no significant differences found among sites or between sexes for any of the plant species, despite the fact that the statistical power of the univariate analyses were high (0.48 - 0.98).

Resource Use and Availability

Eight of the original 17 sites on Boca Chica/Geiger Key were used to determine habitat selection (Table 5.4). Nine sites could not be included in the analysis because either there were no pellets present during 1 of the surveys or 1 of the habitat types was missing. To simplify the analysis data, the 2 years of data were combined and habitat selection was determined by season.

The majority of the overall chi-square goodness-of-fit statistics were significant ($P < 0.05$) for all of the sites during the 3 seasons. Goodness-of-fit

comparisons indicated that habitat selection occurred at least once at all of the sites, and the pattern of selectivity did not appear to vary strongly among seasons. In all 3 seasons, rabbits significantly used mid-marsh vegetation (Borrichia sp. and Sporobolus virginicus) and high marsh vegetation (mainly clump grasses) more than expected and used hammocks and low marshes less. The over all rank of habitat use based on the fecal pellet distribution was: mid-marsh > high marsh > hammock > low marsh.

Habitat Model

Ten variables were used in the 2 DFAs (Table 5.5). All of the habitat variables were either normal without a transformation or became normal after the transformation (Table 5.5). None of the variables were significantly inter-correlated. The test for homogeneity of within-group covariance matrices was not significant ($\underline{X}^2 = 22.75$, $\underline{df} = 46$, $\underline{P} > 0.36$), indicating that a pooled covariance matrix and a linear discriminant function analysis should be used (Morrison 1976).

Four variables (DPopulation, Area, DResidence and MaxHgt) (Table 5.6a) were included in the stepwise DFA comparing empty and occupied sites. Only 2 of the variables, DPopulation and DResidence, differed significantly between empty and occupied sties (Table 5.7). Empty sites were more isolated from other populations but closer to human dwellings. The discriminant

function based on the 4 variables classified 93% of the sites correctly (3 empty sites were classified as being occupied). The jackknife procedure classified 91%, indicating a fairly accurate model. One empty site was misclassified as being occupied; 3 occupied sites were misclassified as being empty.

Four variables were included in the stepwise DFA comparing variably occupied sites to the consistently occupied sites (Clump, DPopulation, MaxHgt, and Borrichia; Table 5.6b). Consistently occupied sites had more clump grasses and significantly higher ground vegetation (Table 5.7). Ninety-seven percent of the sites were correctly classified by the model; 1 consistently occupied site was misclassified as being variable. The jackknife classification rate was also high 95% of the sites were classified correctly.

Potential Reintroduction Sites

Seven of the 17 currently empty sites were classified as being potentially "consistently occupied" habitat sites using the discriminant function and the adjusted inter-population distances (assuming multiple reintroductions on a key). Three of these sites that were classified as being consistently occupied occurred on North Sugarloaf, and 1 each occurred on Cudjoe Key, Middle Torch Key, Big Torch Key and Noname Key.

Discussion

Metapopulation Structure

In the comparison of occupied sites (consistently and variably) and empty patches, the metapopulation structure of S. p. hefneri conforms to the classic definition of a metapopulation (Levins 1969, Hanski and Gilpin 1991). Nearly all patches that are below a maximum inter-patch distance are occupied and patches of all areas are occupied. Lack of a minimum area effect may be due to the methods for patch identification; habitat patches were included in the study only when they exceeded 0.5 ha.

Few good examples of classic metapopulations in nature exist in the literature (Harrison 1991, 1994). This may be a function of the duration of most population studies and scarcity of larger-scale research; otherwise, most systems studied are not true metapopulations. Species that have been found to exist in a classic metapopulation may have some unifying life-histories and behaviors (Murphy et al. 1990), although debate exists as to what these characteristics include (see Harrison 1994). Small-bodied, short-lived species with high reproductive rates (r-selected species) appear to be the most likely candidates for classic metapopulations (Murphy et al. 1990), because such species generally are good colonists and have exceptional dispersal abilities (Harrison 1994). The Lower Keys marsh rabbit fits this description well, as do many species of small mammals, invertebrates, and annual plants.

Harrison (1991, 1994) and Thomas (1994) suggested that species that inhabit early successional habitats that tend to be temporally patchy are more likely to exist in true metapopulations; Murphy et al. (1990) extended this to all species that display strong habitat specificity to a habitat that is fragmented. The marsh rabbits' high marsh - transition zone habitat may differ from stricter definitions of early successional habitat because it does not readily succeed to other habitats. Frequent disturbances from tidal inundation and storms, maintains the habitat over time. However, the Lower Keys marsh rabbit is highly habitat specific, and high marshes are highly fragmented in the Lower Keys. This fragmentation is mainly due to development.

Further examination of the consistently and variably occupied patches indicates that not all patches appear to be of equal value in terms of reproductive potential. Some of the variable patches may be sinks supported by nearby source populations. However, not all of the variable patches were sinks and not all of the consistently occupied sites were sources, indicating that habitat quality is not the only factor elucidating the reproductive potential of a patch. Local extinctions that occurred at the variable sites may have been partly random, and perhaps all sites are variable if a long enough study was conducted.

Habitat Use

Three different temporal and spatial scales provided complementary information on marsh rabbit habitat use. Marsh rabbits forage, nest, and hide in the dense ground vegetation of the transition zone. With some exceptions, S. p. hefneri appeared to feed on the plant species most abundant in its habitat. The major plant species in the rabbit's diet did not appear to vary among sites, between the wet and dry seasons (with one exception), or between males and females. These results differ from the majority of leporid dietary studies.

Few studies have investigated the effect of site on diet. Wallage-Drees et al. (1986) found that the diets of Oryctolagus cuniculus differed among sites. These sites varied greatly in their vegetative composition; a portion of the sites were in woodlands, while others were in heathlands and abandoned arable fields. In contrast, S. p. hefneri is very specialized in its habitat use. Most Lower Keys marsh rabbits inhabit the transition zone. Vegetation in transition-zone areas may vary in proportion between sites but is similar in composition. The dietary requirements of the marsh rabbit may only be met in the transition-zone areas in the Lower Keys.

Seasonal changes in leporid diets have been extensively documented (Cervantes and Martinez 1992, Chapman et al. 1982). In most of these studies, the climate and vegetation changed extensively between seasons. The weather in the Lower Keys is relatively invariant. The variation in the proportion of S.

spartinae in the rabbit's diet is probably due to new growth during the wet season.

Although marsh rabbits eat vegetation in proportion to its abundance, they spend a disproportionate amount of time in the mid- and high marsh. This may indicate that marsh rabbits use the mid- and high marsh for cover while using all areas for foraging. Both the mid- and high marsh contain thick ground cover (Borrichia in the mid-marsh and Spartina and Fimbrystylis in the high marsh). In addition, all nests were found in the high marsh (see Chapter 3).

On a larger scale, the habitat model agreed with the habitat use/ availability results. The model indicated that thick ground cover (especially clump grasses and B. frutescens) and distance between populations were important factors in determining how consistently a habitat patch was occupied. The thick grasses and forb provide the necessary cover for marsh rabbits to nest and escape from predation. Severe predation may reduce population size and increase the chance of stochastic demographic extinction (Gilpin and Soulé 1986). For small-to-medium size herbivores like the marsh rabbit, predation may be the most important factor in determining local abundance (Chapman et al. 1982).

Additionally, patches within close proximity of other occupied patches benefit from emigration of individuals via the "rescue effect" (Brown and

Kodric-Brown 1977) in the context of classic island biogeography, or "internal rescue effect" as it is applied to local patches within a metapopulation (Hanski 1982, Gotelli 1991, Holt 1993). If population numbers have been lowered at a certain patch, new emigrants may reduce population variability, increasing the persistence time of the local population.

Any plans to reintroduce the Lower Keys marsh rabbit should include inoculating near by, multiple patches simultaneously. Not all of the patches used in the reintroduction effort have to be high quality because even the variably occupied patches were capable of supporting marsh rabbits that produced young. Saddlebunch, Big Torch, and Middle Torch Keys all contain multiple habitat patches. Each Key contains at least 1 patch that was classified as being a "consistently occupied" patch. These Keys should be given the highest priority for proposed reintroduction sites.

In conclusion, for S. p. hefneri, habitat quality and incidence-function variables (area and isolation) interact to determine patch occupancy. Not all occupied patches are of the highest habitat quality, and not all of the variable or empty patches are empty because of low habitat quality. Several of the empty habitat patches are sufficiently good habitat to support marsh rabbits, but are too isolated from currently occupied habitat patches to sustain populations. Overall, the Lower Keys marsh rabbit metapopulation did appear

to be closest to the classic metapopulation in structure. Implications of these conclusions will be further examined in Chapter 7.

Table 5.1--Relative density (%) each plant species in fecal pellet group samples (N = 40) of Sylvilagus palustris hefneri.

Plant species and family	X	SE
Sporobolus virginicus--Poaceae	35.74	5.21
Spartina spartinae--Poaceae	17.33	3.87
Laguncularia racemosa--Combretaceae	10.25	2.49
Borrichia frutescens--Asteraceae	8.40	1.51
Rhizophora mangle--Rhizophoraceae	6.81	1.97
Andropogon glomeratus--Poaceae	6.14	2.04
Eleocharis cellulosa--Cyperaceae	3.75	1.63
Muhlenbergia filipes--Poaceae	2.27	1.32
Typha latifolia--Typhaceae	2.10	0.77
Coccoloba uvifera--Polygonacea	1.35	0.81
Fimbristylis castanea--Cyperaceae	0.76	0.38
Jacquinia keyensis--Theophrastueae	0.75	0.30
Salicornia virginica--Cheropodiaceae	0.63	0.31
Sesuvium maritimum--Aizoaceae	0.63	0.10
Avicennia germinans--Avicennianceae	0.38	0.23
Baccharis halimifolia--Asteraceae	0.31	0.18
Erithalis fruticosa--Rubiaceae	0.24	0.17
Fimbristylis spathacea--Cyperaceae	0.23	0.23
Maytenus phyllanthoides--Celastraceae	0.17	0.17
Unidentified material	1.64	0.50

Table 5.2--Ground cover for the 19 most abundant species measured in five transition zone habitat patches in the Lower Keys of Florida. An asterisk following the plant species indicates a species not found in the rabbit's diet.

Plant species and family	X	SE
Spartina spartinae--Poaceae	17.40	8.49
Sporobolus virginicus--Poaceae	14.60	4.31
Borrichia frutescens--Asteraceae	8.40	3.80
Monanthochloe littoralis*--Poaceae	4.40	1.94
Andropogon glomeratus--Poaceae	4.20	2.01
Fimbristylis castanea--Cyperaceae	4.20	1.91
Conocarpus erecta*--Combretaceae	2.80	0.74
Muhlenbergia filipes--Poaceae	2.60	1.19
Pithecellobium guadelupense*--Fabaceae	2.00	2.00
Fimbristylis spathacea--Cyperaceae	1.60	1.17
Salicornia virginica--Cheropodiaceae	1.40	0.93
Laguncularia racemosa--Combretaceae	1.20	0.20
Avicennia germinans--Avicennianceae	1.00	0.32
Coccoloba uvifera--Polygonacea	1.00	0.63
Rhizophora mangle--Rhizophoraceae	1.00	0.32
Typha latifolia--Typhaceae	1.00	1.00
Eleocharis cellulosa--Cyperaceae	0.80	0.49
Sesuvium maritimum--Aizoaceae	0.80	0.80
Baccharis halimifolia--Asteraceae	0.40	0.40

Table 5.3--Results of univariate analysis of variance on arcsine-transformed percentage relative density of Sporobolus virginicus (Sv), Spartina spartinae (Sp), Laguncularia racemosa (Lr) and Borrichia frutescnes (Bf) in the fecal pellets of S. p. hefneri in the Lower Keys of Florida.

		Sv		Sp		Lr		Bf	
Source	df	F	P	F	P	F	P	F	P
Site	5	0.87	ns	1.38	ns	1.15	ns	0.97	ns
Season	1	2.39	ns	11.61	**	2.27	ns	1.26	ns
Sex	1	0.21	ns	1.26	ns	0.04	ns	0.01	ns
Season by sex	1	15.71	**	6.24	*	2.19	ns	0.00	ns

(* $0.05 \geq P > 0.01$; ** $0.01 \geq P > 0.001$; ns = $P > 0.05$)

Table 5.4--Goodness-of-fit test for habitat use by Lower Keys marsh rabbits on Boca Chica/Geiger Key. A "+" denotes that a habitat was used significantly more than expected, a "-" refers to a habitat that was used significantly less, and a "0" means the habitat was neutral with respect to use according to the Bonferonni confidence intervals.

March					
Site	X^2	Low marsh	Mid-marsh	High marsh	Hammock
1	6.73	0	0	0	0
4	8.14	0	0	0	-
8	23.02	0	+	0	0
9	3.95	0	0	0	0
10	14.72	-	0	+	0
11	15.13	-	+	0	0
12	31.42	-	0	+	0
13	49.38	-	+	0	0
Total		4(-)	3(+)	2(+)	1(-)

July					
Site	X^2	Low marsh	Mid-marsh	High marsh	Hammock
1	5.91	0	0	0	0
4	10.33	0	0	0	0
8	81.07	-	0	0	0
9	1.03	0	0	0	0
10	9.75	-	0	+	0
11	11.05	-	+	0	0
12	30.17	-	0	+	0
13	41.28	0	+	0	-
Total		4(-)	2(+)	2(+)	1(-)

Table 5.4 (continued).

		November			
Site	X^2	Low marsh	Mid-marsh	High marsh	Hammock
1	30.42	-	+	0	-
4	4.02	0	0	0	0
8	17.05	0	+	0	-
9	3.95	0	+	0	0
10	8.97	-	0	+	0
11	11.46	-	0	0	-
12	31.42	-	0	+	0
13	5.43	0	0	0	-
Total		4(-)	3(+)	2(+)	4(-)
Grand Total		12(-)	8(+)	6(+)	6(-)

Table 5.5--Variables used to measure characteristics of marsh rabbit habitat in the Lower Keys of Florida.

Variable abbreviation	Variable	Mode of measurement	Range	Trans-formation*
GCover	Ground Cover	proportion of 10 transects occluded below 1.5 m	30-98%	S
CCover	Canopy Cover	proportion of 10 transects occluded above 1.5 m	2-81%	S
Borrichia	Borrichia frutescens cover	proportion of 10 transects occluded at ground level	0-60%	S
Clump	Clump grass cover	proportion of 10 transects occluded by Spartina spartinae, Fimbrystilis sp. and Cladium jamaicensis	0-87%	S
MaxHgt	Average maximum height	average maximum height of ground vegetation measured in 0.25-m intervals in the 1st, 3rd, and 5th meters of each transect	6.5-62.0 cm	N
H'	Plant diversity	Shannon-Weaver diversity index based on ground and canopy species present in 10 transects	0.55-2.17	N
Area	Area of habitat patch	aerial photograph	0.3-43.7 ha	L
DPopulation	Distance from edge of site to nearest rabbit population	aerial photograph	40-6066 m	L

Table 5.5 (continued).

DResidence	Distance from edge of site to nearest occupied domicile	aerial photograph	1-6000 m	L
DWater	Distance from edge of site to body of water	aerial photograph	1-1000 m	L

* Transformations applied to data to achieve normality: S = square-root, L = $\log_{10}$, N = no transformation needed, data already normal.

Table 5.6a--Results from a stepwise discriminant function analysis of 10 habitat variables measured on "occupied" and "empty" marsh rabbit habitat in the Lower Keys of Florida.

Habitat Variable	Step entered	Partial R^2	F	P
DPopulation	1	0.56	73.26	0.0001
Area	2	0.12	7.63	0.0007
DResidence	3	0.08	5.01	0.01
GCover	4	0.05	2.97	0.09

Table 5.6b--Results from a stepwise discriminant function analysis of 10 habitat variables measured on "variably" and "consistently" occupied marsh rabbit habitat in the Lower Keys of Florida.

Habitat Variable	Step entered	Partial R^2	F	P
Clump	1	0.60	60.48	0.0001
DPopulation	2	0.27	14.29	0.0005
MaxHgt	3	0.08	3.24	0.05
Borrichia	4	0.09	3.78	0.04

Table 5.7--A comparison of habitat measurements between occupied and empty marsh rabbit habitat in the Lower Keys of Florida.

Habitat variable (Unit)	Occupied habitat (n=42)		Empty habitat (n=17)		Test statistic*	P
	X(SE)	Untransformed	X(SE)	Untransformed		
GCover(%)	7.7(0.2)	59.3	8.0(0.3)	64.0	1.12 (T)	0.27
CCover(%)	3.7(0.2)	13.7	3.8(0.5)	14.4	-0.44 (U)	0.66
Borrichia(%)	2.3(0.2)	5.3	1.5(0.5)	2.3	-2.36 (U)	0.02
Clump(%)	4.4(0.3)	19.4	4.5(0.6)	20.3	0.15 (T)	0.88
MaxHgt(cm)	22.2(1.7)	22.2	28.7(4.2)	28.7	1.10 (U)	0.27
H(#)	1.4(0.1)	1.4	1.3(0.1)	1.3	-1.35 (T)	0.19
Area(ha)	1.6(0.3)	4.8	0.6(0.1)	1.8	-1.15 (T)	0.25
DPopulation(m)	5.8(0.2)	330.3	8.1(0.1)	3294.5	5.78 (U)	0.001
DResidence(m)	5.7(0.4)	298.9	2.9(0.8)	18.2	-3.10 (T)	0.005
DWater(m)	3.0(0.4)	20.1	2.9(0.6)	18.2	-0.20 (U)	0.84

* For all normally distributed variables (or transformed variables) a two-sample t-test (T) was used, a Mann-Whitney U-test using normal approximation (U) was used for all non-normally distributed variables.

Table 5.8--A comparison of habitat measurements between good and marginal marsh rabbit habitat in the Lower Keys of Florida.

Habitat variable (Unit)	Constitent habitat (n=22)		Variable habitat (n=20)		Test statistic*	P
	X(SE)	Untransformed	X(SE)	Untransformed		
GCover(%)	8.2 (0.2)	67.2	7.2 (0.2)	51.8	-3.65 (T)	0.008
CCover(%)	3.6 (1.3)	13.0	3.9 (1.2)	15.2	1.04 (U)	0.31
Borrichia(%)	2.3 (0.3)	5.2	2.2 (0.3)	4.8	-0.17 (U)	0.86
Clump(%)	5.9 (0.3)	34.8	3.1 (0.2)	9.6	-7.73 (T)	0.001
MaxHgt(cm)	26.4 (3.2)	26.4	18.3 (1.1)	18.3	-2.47 (U)	0.02
H(#)	1.5 (0.1)	1.5	1.7 (0.1)	1.7	0.99 (T)	0.32
Area(ha)	1.8 (0.5)	5.8	1.7 (0.8)	5.5	-0.14 (U)	0.89
DPopulation(m)	5.5 (0.3)	244.7	6.1 (0.2)	445.9	1.93 (U)	0.06
DResidence(m)	5.8 (0.6)	330.3	5.5 (0.6)	244.7	-0.34 (T)	0.73
DWater(m)	3.5 (1.5)	33.1	2.7 (0.5)	14.9	-1.08 (T)	0.28

* For all normally distributed variables (or transformed variables) a two-sample t-test (T) was used, a Mann-Whitney U-test using normal approximation (U) was used for all non-normally distributed variables.

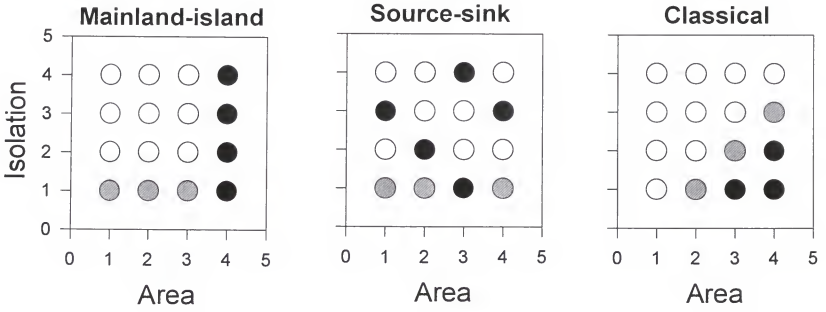


Figure 5.1 The 3 types of metapopulation structure: mainland-island, source-sink, and the stepping stone model a form of the classical metapopulation. The black circles are consistently occupied sites. Grey are variably occupied sites and the white circles are empty sites.

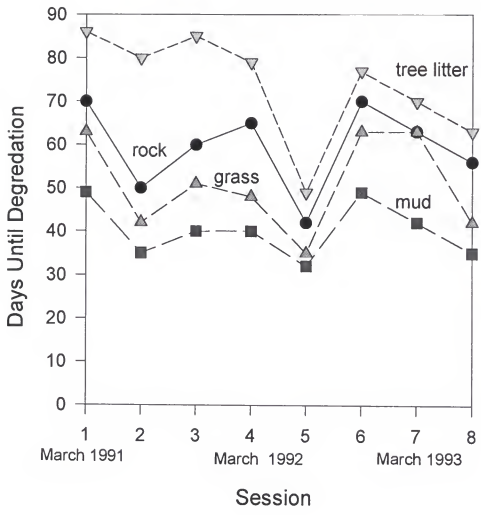


Figure 5.2 Number of days until the first Lower Keys marsh rabbit (Sylvilagus palustris hefneri) pellet decayed. One group of 25 pellets was placed in each of 4 settings (in tree litter, on rocks, in grass, and in mud) and observed daily.

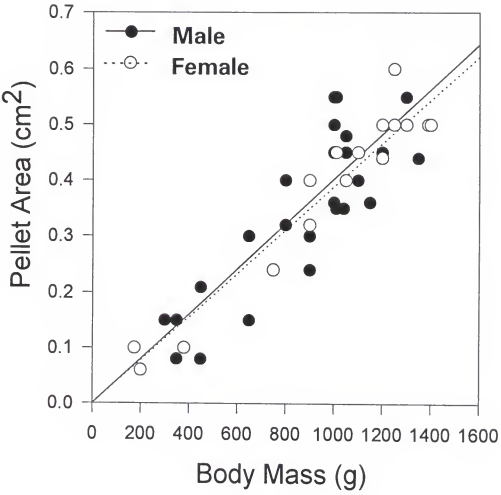


Figure 5.3 Average pellet size (in area cm^2) in relation to body mass (g) of 53 Lower Keys marsh rabbits (Sylvilagus palustris hefneri) trapped on Boca Chica and Saddlebunch Keys.

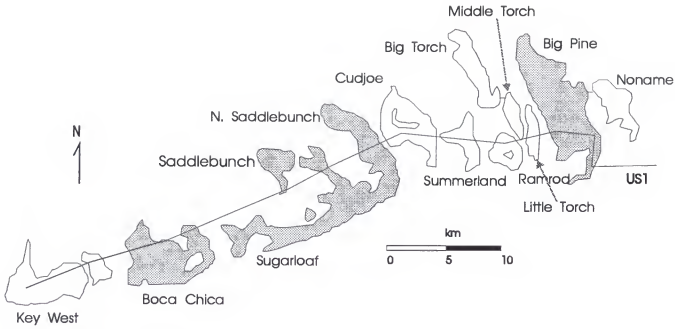


Figure 5.4 The current distribution of the Lower Keys marsh rabbit (Sylvilagus palustris hefneri) by Key. The stipled keys are occupied; white keys are unoccupied.

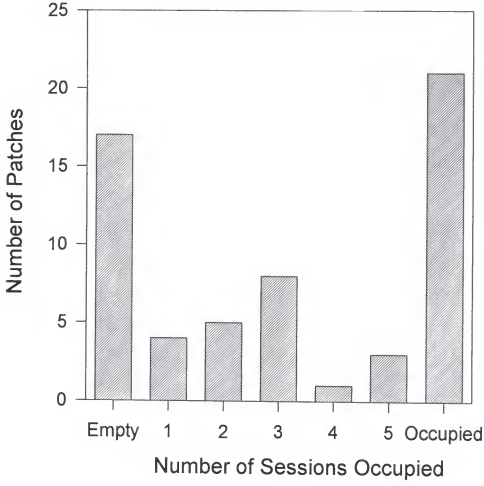


Figure 5.5--Number of sessions (from session 3-8) occupied by the Lower Keys marsh rabbit (Sylvilagus palustris hefneri) at each of the 59 transition-zone sites.

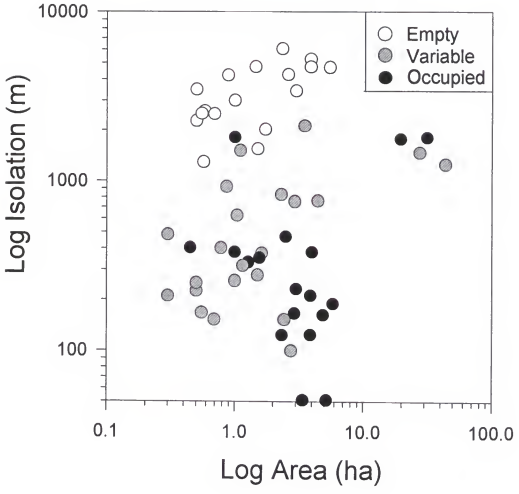


Figure 5.6 Fifty-nine sites plotted with respect to Lower Keys marsh rabbit (Sylvilagus palustris hefneri) occupancy by $\log_{10}$ area (ha) and $\log_{10}$ isolation (m). Empty patches never had marsh rabbits present, variable patches had marsh rabbits during at least 1 session, and occupied sites had rabbits during all of the sessions.

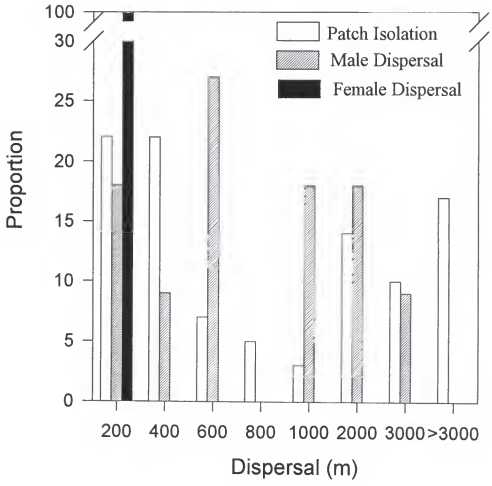


Figure 5.7 Average distance between a patch and the nearest occupied patch (patch isolation) for the 59 patches, in comparison to the dispersal distances of the 6 female Lower Keys marsh rabbits (Sylvilagus palustris hefneri) and the 11 male.

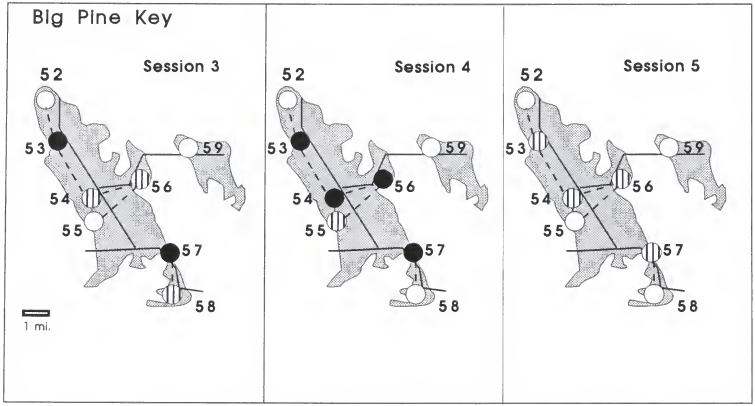


Figure 5.8 Patch occupancy by Lower Keys marsh rabbits (Sylvilagus palustris hefneri) during the last 6 pellet sampling sessions. A solid circle indicates an occupied patch, a dashed circle represents a patch occupied by adults only, and an open circle indicates a vacant patch. Dashed lines between patches indicate patches within dispersal distance from each other. The solid lines are roads.

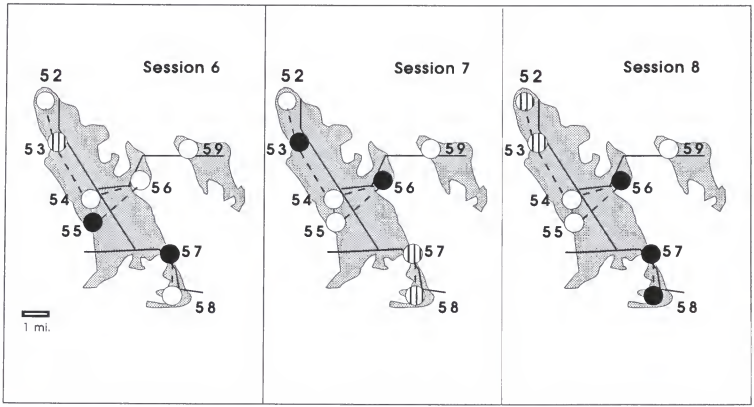


Figure 5.8 (continued).

CHAPTER 6
POPULATION VIABILITY ANALYSIS

Introduction

The process of conducting a population viability analysis (PVA; Soulé 1987) involves building a model that makes probabilistic predictions about a species' future (Ginzburg et al. 1982, Shaffer 1990). Most models use population simulation or analysis based on existing data to make these predictions. The challenge in developing a PVA is creating a model that captures all of the important aspects of a species' ecology while using only realistically measurable parameters (Eberhardt 1987, Boyce 1992).

This process is further complicated when the population to be modeled exists in discrete subpopulations. If these subpopulations are related through inter-subpopulation movements that have the potential to augment or recolonize small or extinct subpopulations, then the PVA must include this metapopulation structure (LaHaye et al. 1994).

Multiple Levels of Population Viability Analysis

A PVA that incorporates metapopulation structure can involve processes that occur at 3 increasing spatial levels: subpopulation (patch), between

populations, and metapopulation. The subpopulation level (or patch) is the traditional domain of PVAs that involve a single population.

Most single-population PVAs are conducted on small populations and require that both stochastic and deterministic processes be examined (Gilpin and Soulé 1986, Wilcox 1986, Lacy and Clark 1990). Small populations are more likely to be at risk of extinction due to stochastic variation than are large populations. Stochastic perturbations in small populations can affect the genetic composition (loss of genetic variability, inbreeding depression) or the demographic composition (sex, age ratios) of a population (Shaffer 1981). Variation in the environment (climatic variation, natural catastrophes), is also random but affects small populations only slightly more than larger ones.

Deterministic causes of extinction include Diamond's "evil quartet": overkill, habitat destruction, invasion by introduced predators or competitors, and food-web collapse (Diamond 1984, 1989). In addition, climatic change (Nunney and Campell 1993) may be deterministic and disease may be stochastic or deterministic depending on its extent and the impact it has on the population (Aguirre and Starkey 1994). Deterministic extinction can occur regardless of population size, if all of the population is effected. For most species, deterministic processes play a larger role in the original decline of the species, while stochastic process are responsible for the extinction after the decline (Caughley 1994). Both stochastic and deterministic phenomena may

interact via feed-back loops leading to potential extinction via "extinction vortices" (Gilpin and Soulé 1986).

Interactions between patches also can be an important component of the PVA. Dispersal rates, the mechanisms behind dispersal, and the impact of habitat on dispersal can effect the amount of interchange between populations. Individuals moving between patches may increase an the persistence time of an occupied patch by augmenting the population and decreasing the chance for stochastic extinction (rescue effect; Brown and Kodric-Brown 1977). The dispersing individuals may also recolonize empty patches, if both males and females or pregnant females move (in a sexual species). Incorporating inter-patch dynamics requires using spatially explicit metapopulation structure.

The third spatial level, metapopulation dynamics, considers the inter-relation between patch extinction and recolonization. For a metapopulation to persist, the patch recolonization rates must exceed patch extinction rates (Levins 1970, Hanski and Gilpin 1991). The inter-patch movements described above will determine recolonization rates, but metapopulation persistence is largely dependent on a lack of correlation among populations in extinction rates (Murphy et al. 1990, Thomas and Jones 1993). Environmental variation and catastrophes can cause synchronous variations in population densities (Quinn and Hastings 1987, Gilpin 1988, Hanski 1989, Stacey and Taper 1992). If all patches are subjected to the same adverse environmental conditions at the

same time, then patch extinctions may be correlated, leaving few or no source populations to colonize the extinct patches.

Population Viability Analysis Models

Most metapopulation models (e.g., Nisbet and Gurney 1982, Hanski 1985, 1991, Hastings and Wolin 1989, Hastings 1991, Verboom et al. 1991, Gyllenberg and Hanski 1992, Nee and May 1992) predict metapopulation persistence based on phenomena that occur at the metapopulation level only (Hanski 1994). Most of these models are theoretical in nature, and the parameters can not be readily measured in the field. A few models (Fahrig and Merriam 1985, Hanski and Gyllenburg 1993), incorporate the inter-population level and the metapopulation level phenomena, creating spatially realistic models that require only modest amounts of data to construct. These models provide information on metapopulation dynamics of real populations but are less useful in making management decisions. Models that incorporate all 3 levels require substantially more information but may be used to test hypotheses regarding threats to the species at all 3 levels.

Several simulation models are currently available that combine stochastic birth and death process models (Richter-Dyn and Goel 1972, Goodman 1987), differing migration rates based on spatially explicit patch structure and extinction and recolonization (correlated or uncorrelated).

VORTEX (Lacy 1993) and RAMAS/metapop (Akçakaya 1994) both provide estimations about the persistence of a metapopulation using a Monte Carlo simulation algorithm to generate stochasticity. VORTEX is slightly less flexible in its treatment of population growth and is limited in the number of subpopulations that can be modeled at once.

Costs and Benefits of Using a PVA Model

Although most scientists and managers consider a detailed PVA to be a useful tool in making management decisions (Salwasser et al. 1984, Marcot and Holthhausen 1987, Shaffer 1990), these models have recently come under criticism. For many species, data are not currently available to conduct an in-depth PVA, and by the time it is collected the species may be extinct (Maguire 1991, Boyce 1992). Some population dynamics such as density dependence are poorly understood, regardless of the parameters measured in the field (Hassell 1986). This lack of knowledge can severely detract from the most well-developed PVA model. For other species, conducting a PVA may estimate how long the species will persist but not indicate why the species is declining (Caughley 1994). Managers, lawyers and the public often consider the predictions of PVAs as facts, and do not give credence to the variance and limitations of the model (Barthouse et al. 1984). Finally, few PVA models are

ever validated and therefore it is difficult to determine which model approaches are most successful (Grant 1986).

Despite these problems, PVA has been found to be a useful management tool for a number of species (grizzly bear, Suchy 1985; northern Spotted owl, LaHaye et al. 1994). The strongest potential of PVA is in the development of adaptive management strategies (Holling 1978, Walters 1986, Lee 1993) to recover endangered species. A well-developed PVA can refine multiple hypotheses about the impact of multiple management tactics. Small-scale management techniques can be attempted at different (sub)populations, the (sub)populations monitored, the PVA model validated, and then the most successful suite of management techniques applied to all of the populations.

The main objective of this chapter is to develop a PVA model for the Lower Keys marsh rabbit (Sylvilagus palustris hefneri). This model will make predictions about the persistence of the subspecies under a variety of potential scenarios and management techniques. This information will be used to make recommendations about the direction of future research and management of this subspecies.

The Lower Keys marsh rabbit is an endangered subspecies occurring in a "classical" metapopulation structure. It is believed to be declining during recent years (Howe 1988) and was only protected 4 years ago. Since the

formal listing, habitat destruction has abated somewhat, although development of the rabbits habitat is still possible.

Methods

The RAMAS/metapop (Akçakaya 1994) simulation model was used for the PVA because of its flexibility and ability to incorporate a large number of populations. Processes occurring at all 3 spatial levels were incorporated in the model. At the level of the population, a life-history table in the form of a Leslie matrix (Leslie 1945) was completed, the impact of demographic and genetic stochasticity assessed, the form of the population growth curve was estimated, and the initial abundances for each population were estimated. At the between-population level, the number and age of the individuals moving between populations was determined, and the spatial structure of the metapopulation and the impact this has on inter-population movements was estimated. At the metapopulation level, the degree of correlation between population density was estimated.

Population-level Parameters

A stage rather than age Leslie matrix was used based on the results of Chapter 3, which suggested that S. p. hefneri differs in survival and reproduction depending on the developmental stage. Five stages were used:

nestlings (0-3 months), juveniles (4-7), subadults (8-10), first-year adults, and second- (and older-) year adults. Survivorship was estimated using a combination of live-trapping and radio-telemetry, as was reproductive effect per female (see Chapter 3). Males and females were combined when determining all rates.

Demographic stochasticity (e.g., sex ration, demographic structure) was studied by monitoring marsh rabbit populations at 5 patches of habitat. Genetic variation was determined by taking blood from the ears of marsh rabbits and performing starch-gel enzyme electrophoresis (as described in Chapter 3).

Determining whether population growth of S. p. hefneri is dependent or independent of density provided a challenge. Detecting density dependence in natural populations is difficult because of the variation caused by stochastic demographic and environmental processes (Burgman et al. 1993). Few studies have actually documented that density-dependence occurs, despite a profusion of studies. Several methods of detecting density dependence using sequential censuses have been developed, but none of these methods reliably test density dependence (Hassell 1986). An experimental manipulation of population density over time is the best way to determine density dependence. However, when working with endangered species, manipulations may be difficult because they may affect the population and because the necessary time may not

be available to conduct such an experiment. Gaston and Lawton (1987) suggest that a qualitative analysis of the population dynamics and life history of a species might be used to infer if density dependence could occur. For the purposes of this model, it was assumed that the rabbit, a short-lived, quickly reproducing mammal, might exhibit some density dependence. The first run of the model incorporated simple density dependence using the logistic equation, where population growth follows the logistic equation until carrying capacity (K) is reach. At carrying capacity the model uses the life-table to predict population growth.

Yet, because of the severe predation pressure (Chapter 3) on the marsh rabbits, population growth might be controlled by the predation, limiting the ability of the Lower Keys marsh rabbit to exhibit density-dependent population growth. The model was additionally run without density dependence, using the exponential equation in conjunction with the life table to predict population growth.

To determine the carrying capacity for the density-dependent growth, the number of males that could fit into a patch was calculated by assuming non-overlapping core areas. For areas of "consistently occupied" habitat (Chapter 5), the size of the male core area was the mean core area calculated in Chapter 4 plus one standard deviation. For areas of "variably occupied" habitat, the size of the male core area was this mean core area minus one

standard deviation. Assuming a one-to-one ratio between males and females, the number of males was doubled to reach the carrying capacity of adults. Assuming a stable age distribution, the number of subadult, juveniles and nestlings was estimated and added to the adult carrying capacity.

To determine the initial abundance of rabbits at each site, pellet counts were used throughout the study. With knowledge about the distribution of pellets, the number of pellets produced by a rabbit a day and the pellet persistence rate (calculated as 30 days in Chapter 5), fairly accurate abundances can be obtained (Wood 1988). For the purposes of this study, only adult pellets were counted (those pellets with an area >0.4 cm^2, see Chapter 5). Presence or absence of juvenile pellets was recorded, but these pellets were not included in the density estimates.

To determine the number of pellets each rabbit produced in 1 day, 4 trapped adult rabbits (2 male, 2 female), were given a collection of natural vegetation and placed for 24 hrs in a rabbit cage with a removable pan beneath the mesh floor. This procedure was repeated 3 times a year (March, July, and November) to document the effect of climate and rabbit age during late dry season, mid-wet season, and the transition time between wet and dry seasons.

Reliability of pellet counts may be affected by the patchy distribution of pellets, which can bias the counting technique. To identify a reliable method, during the first pellet-sampling period sampling units (SU) of 2 sizes were used

at all of the grids. The SU consisted of concentric 0.5-m- and 1.0-m-radius circles around each permanent marker. Inside these circles, pellets were removed, and then new pellets were counted after a specified amount of time. To determine which SU size was optimal, the distribution pattern of pellets was fitted to a Poisson distribution model. The Poisson distribution furnishes values expected for a random dispersion pattern. When a chi-square goodness-of-fit test is used to compare the 2 distributions, a significant result indicates that the sample is non-random. The optimal sampling unit will be most likely to produce a random distribution of pellets.

Once the preferred SU was selected, the following equation was used to estimate rabbit density:

$$D = \frac{(10{,}000\ m^2/ha) * X}{T * R * A}$$

where: D = density of rabbits (rabbits per ha),

X = mean number of pellets per SU,

T = time between pellet removal and pellet counting,

R = defecation rate (number of pellets dropped per rabbit per 24-hr day)

A = surface of each SU (m^2).

The defecation rate (R) was determined as described in the previous section, "pellet production". The number of days between pellet removal and counting (T), was determined to be more than 30 days in Chapter 5. Thirty days was used as the sampling interval.

Density estimation was attempted at the permanent fecal pellet-sampling grids that were established at each of 59 patches of transition-zone habitat in the Lower Keys. The grid was designed to fit into the smallest patch and consisted of a square of 7 x 7 stations at 15-m intervals, marked with permanent flags. The grids were surveyed 3 times per year: March (late dry season), July (mid-wet season), and November (transition between wet and dry) from March 1991 to July 1993. Each survey consisted of pellet removal within a radius of 0.5 m at each station followed by a pellet count 1 month later. Because some of the grids were occasionally disturbed by vehicles, these grids were examined only for pellet presence or absence. At several privately-owned sites and sites that were deemed "sensitive" by the Navy, access was limited and the time necessary to thoroughly count the pellets was not available. These sites also were only examined for presence or absence of pellets.

To determine the initial abundances for the model, all of the density estimations collected during session 3 were used. Session 3 was chosen because the most sites were censused during that time. To calculate initial

abundance, the density of adult rabbits was multiplied by the area of the patch. If juvenile pellets were found at that grid during the census, then a stable age distribution was assumed and the number of subadults, juveniles and nestlings was included. If no juvenile pellets were found, then it was assumed that the rabbits at that patch had not produced any young and only the number of adult rabbits was used.

For patches where density estimates were not possible to obtain, the carrying capacity of the patch was used as the initial abundance. Although this may have been higher than the actual number of rabbits, these patches were all small and less likely to have a major impact on the estimate of total abundance.

Inter-population Level Parameters

To determine the amount of movement between populations, 6 populations of marsh rabbits on Boca Chica Key and Saddlebunch keys were trapped. Radio-collars were placed on all rabbits >300 g. This ensured that rabbits of all developmental stages (except for the altricial nestlings) were represented. Radio locations were ascertained 3 times per week, or daily if it appeared the rabbit was making a long-distance movement. The distance and type of habitat of each long-distance movement was determined (see Chapter 4), including the crossing of major barriers (e.g., bodies of water, roads, runways).

Metapopulation Parameters

To determine if the variation in population densities was correlated among populations, a multivariate, repeated-step analysis of variance (MANOVA) was performed on the density estimations collected during the 8 sampling sessions (PROC AUTOREG, SAS/ETS, Sas Institute 1984). Estimated abundances of each of the populations over the 8 sessions was compared to the other populations an the same key. Sites that never supported any marsh rabbits were removed from the analysis.

The Model

Using the parameters described above, the simulation was repeated 1,000 times for each scenario (described below) and run for 50 years. Most PVA models are run for 100 years however, the predicted increase in sea level rise for south Florida (Ross et al. 1994) implies habitat changes and precludes such a long-term outlook. To test the sensitivity of the input parameters, all of the elements in the Leslie matrix were varied. This includes survivorship in each of the 5 stages and reproduction in the adults.

Scenarios

Each scenario is described in depth below, but the specific numerical modifications in the parameters for each scenario are listed in Table 6.1. The first 2 simulations used the original parameters but differed in the way they simulated population growth. The first simulation used the logistic equation for population growth; the second used the exponential. After comparing the results of the simulation with knowledge about the biology of S. p. hefneri, 1 simulation was chosen to be used in the scenarios.

Scenario #1- Decrease Predation.

(a). Predator control leads to a 25% decrease in mortality in each stage. This would require a 50% reduction in the current amount of cat predation. This would be likely to occur if the house-based and feral cats (Felis catus) were removed and prevented from hunting in marsh rabbit habitat. Some predation would probably occur before cats were captured in the trap but the overall mortality rate would decrease. The radio-telemetry study conducted on the Lower Keys marsh rabbit (see Chapter 3) found that cats were the major predator of juvenile, subadult, and adult rabbits. It is assumed that nestling rabbits also would be vulnerable to cat predation.

(b). Predator control leads to a 50% decrease in mortality at each stage. This would require complete extermination of all cats in marsh rabbit habitat

and a reduction in mortalities attributable to raccoons. Raccoon population reduction might occur when supplemental food sources are eliminated (i.e., open dumpsters, outdoor pet food).

Scenario #2 - Decrease Road-kills.

All vehicular deaths are prevented. This would mean a roughly 25% increase in the survivorship of subadults and 10% increase in the number of adults. Implementing this management strategy would require strict speed limit reductions, or an over(under) pass for the rabbits to use.

Scenario #3- Reintroduce Rabbits.

Rabbits are reintroduced to all vacant habitat patches. This would entail using captive breeding to produce rabbits to be released to the 17 empty habitat patches (see Chapter 5). The number and stage of the rabbits to be introduced would be determined by calculating carrying capacity for each patch and assuming a stable age distribution.

Scenario #4 - Disease.

(a). A relatively mild disease (e.g. tularemia) that kills some of the infected individuals spreads through the keys. The disease kills animals in the stages that have social contact (i.e., the nestlings and adults). The disease

affects 1 patch at a time, but each patch has 75% chance of getting infected each year. Tulemia epizootics have been observed in a number of rabbit species (Jellison 1969) and may play a role in population regulation (Woolf et al. 1993). The rate of spread between infected populations is not known (Woolf et al. 1993). Infected populations generally pass the disease to most, but not all, nearby populations.

(b). A more severe disease, perhaps similar to the effects of myxamatosis in Australia and Europe on Oryctolagus cuniculus (Chapman and Flux 1990), spreads through the Keys. This disease also kills only the nestlings and adults, but its mortality rate is much higher than the disease described in (a). This disease also affects one patch at a time and with a 75% chance each year.

Scenario #5 - Hurricanes.

(a). A class 3 hurricane directly hits the center of the Lower Keys during the first year of the simulation. The effect is regional, and all keys suffer some mortality. Storm surge inflicts the greatest effect. Mortality is highest for the nestlings and lowest for the adults that can swim. The probability that a hurricane of this strength hits the Lower Keys is <10% each year.

(b). Same scenario as (a), only the hurricane is class 4 and therefore the mortality is higher. Class 4 hurricanes occur less frequently than class 3. The probability of this strength of a hurricane is <5%.

(c). Same scenario as (a) and (b), but the hurricane is class 5 and therefore will cause the greatest amount of mortality. This type of hurricane has a <1% chance of occurring each year.

Scenario #6 - Corridor Destruction.

(a). Corridor habitat is destroyed and this decreases migration by 25%. All patches are affected.

(b). Corridor habitat is destroyed and decreases migration by 50%. All patches are affected.

Scenario #7 - Habitat Destruction.

(a). The largest patch (site 33, 31.5 ha) is destroyed. This patch is privately owned and could potentially be developed.

(b). The 5 largest patches are destroyed. This would include site #33 and 4 large areas on Big Pine. This is a less likely scenario because the 4 large areas on Big Pine currently are protected.

(c). The 10 smallest patches are destroyed. The majority of these patches are on Boca Chica and Saddlebunch Keys. This scenario is very likely, the patches are all owned by the Navy or privately owned.

Results

Population Parameter Estimations

The Leslie matrix was completed using estimates of survivorship and reproduction given in Chapter 3. Survivorship of nestlings and the standard error was 0.28 (0.17), for juveniles it was higher at 0.75 (0.10), for subadults it was 0.67 (0.14), for first-year adults it was 0.52 (0.09) and for second-year and older adults it was 0.10 (0.12). Reproductive rates were assumed to be the same for first- and second- year adults. The reproductive rate was obtained by multiplying the average female fecundity rate by the survivorship of the stage class and then dividing by 2 to account for males. The rate for first-year adults was 2.19 (0.07) and 1.70 (0.10) for second-year adults.

The marsh rabbit populations did not exhibit evidence of inbreeding depression or low genetic variation. Sylvilagus palustris hefneri had a level of genetic variation similar to large populations of cottontail (Scribner and Warren 1986); genetic effects were not factored into the model. Demographic stochasticity did appear in the marsh rabbit populations. Several populations were so small that at times they occasionally only supported members of the

same sex and these populations eventually went extinct. Demographic stochasticity was incorporated into the model by varying survivorship and reproduction (Akçakaya 1994). The number of survivors for each stage was drawn from a binomial distribution determined by the survival rate and the smaple size. The number of young produced by each stage was drawn from a Poisoon distriubtion.

A careful examination of the life-history parameters in each population revealed that density-dependent growth does not appear to be occurring at the 5 populations from which the data was collected. Populations appeared to be low due to the high mortality, and mortality was high at all of the patches, regardless of rabbit density. However, these were collected only at Boca Chica Key and Saddlebunch Key and could differ at the other keys. Therefore the 2 basic simulations were run, 1 with density dependence and 1 without.

Carrying capacity calculations (by site) for the density dependent population growth ranged from a low of 3 rabbits (all stages) at the smallest site to a high of 596 rabbits at the largest. Adding all the carrying capacities together from all of the habitat patches, a total of 2,917 marsh rabbit (nestling through adult) could occupy the Keys.

Density Estimation

Average defecation rate (R) varied between seasons, ranging from an average of 103.75 pellets/day in July 1993 to 171.0 pellet/day in March 1991 (Table 6.2). Although the data are limited in its temporal scope, marsh rabbits appear to produce fewer pellets in the warmer months and more in the cooler months. Similar results were found in pellet studies of other species of rabbit (Lord 1963).

Using the 30-day sampling period, the defecation rate from the first survey (March 1991), and the 0.5-m-radius sample, 8 of the 13 sites on Boca Chica had a random distribution of pellets (Table 6.3). Using the same constants and the 1-m-radius, only 2 sites had a random distribution of pellets. Therefore, pellet counts from the 0.5-m circle were used for estimating rabbit densities in this and all subsequent surveys.

Of the 39 sites (Appendix C) used in the density estimation, 9 did not appear to have been used or inhabited during the study. A comparison of carrying capacities with estimated total abundances at the patches revealed that over two thirds of the patches were under carrying capacity (Table 6.4). The estimated total adult marsh rabbit population size fluctuated widely between a low of approximately 100 individuals to a high of nearly 300 (Figure 6.1). This estimate includes all of the sites used in the density estimate (Appendix A), but it does not include the sites that could not be censused. Changes in the

density of rabbits at the largest site (site 33; Sugarloaf) had a large effect in overall population size. These large fluctuations in the total population size did not appear to be seasonal. The weather during the 2.5 years of the study was normal with respect to temperature and precipitation (Figure 6.2).

Between-population and Metapopulation Parameters

Only subadults made long, one-way movements (see Chapter 4), and 75% of these successfully reached a new patch. Movement distance differed greatly between individuals; males generally moved farther than females. Because in RAMAS/metapop male and female dispersal can not be distinguished, male and female dispersal was pooled. Based on the pooled dispersal data (Chapter 4), it was assumed that if a patch was 50 m or less away from another patch, then it could be reached by 94% of the dispersers. If it was between 50 and l00 m, then 63% could reach it; between 100-500, then 50%. Patches 500 - 1000 m away could only be reached by 19% of the dispersers and patches between 1000-2000 m away could be reached by 6%. For patches >3000 m distant, a migration rate of <0.01 was included, to allow for a rabbit that had superior dispersal ability.

No evidence of inter-population correlation in population size was found using the repeated measures MANOVA. None of the correlations were significant ($P \geq 0.05$), and the highest correlation was $r = 0.65$.

Simulation Results

The simulations using the exponential growth curve and the logistic growth curves predicted nearly opposite outcomes for S. p. hefneri (Figure 6.3). The logistic growth curve simulation predicted that the marsh rabbit metapopulation was stable and would vary around 1,200 rabbits (168 adults). There were approximately 35 patches occupied during any time. The exponential growth curve simulation estimated that S. p. hefneri would go extinct within the next 20-30 years if all the parameters remained the same. Because the total estimated abundances at the patches were predominantly below carrying capacities at all of the sites and the mortality rate estimated from the 5 main sites was high, it was determined that the exponential growth curve was more biologically defensible. Because the exponential growth curve more accurately mimicked population growth and was more conservative, it was used in all of the scenarios.

Since extinction was imminent without increasing mortality or decreasing reproduction, the sensitivity analysis only looked at increases in survivorship and increases in reproduction. Each parameter was varied by increasing it 25% and 50%. None of the variations appeared to stabilize the population around a single point, however, 5 of the manipulations slowed the extinction time to beyond 50 years (Table 6.5). Changes in the nestling survivorship rate and the adult survival rates prolonged persistence the most.

Increasing the survival rate of the juveniles and subadults and increasing reproduction did not produce large changes in the fate of the population.

In scenario #1, the increase in survivorship in all stages by 25 % resulted in a stabilization of the predicted population size and metapopulation occupancy (Figure 6.4). The population varied around 1,200 total individuals occupying approximately 30 patches. When survivorship was increased by 50%, the population exponentially grew to nearly 8,000 individuals, and all patches were eventually occupied.

In scenario #2, elimination of vehicular mortalities only prolonged the persistence time by approximately 10 years (Figure 6.5). Similarly, in scenario #3, when all the currently empty patches were recolonized by a carrying capacity level of marsh rabbits in scenario #1, the population only persisted slightly longer than without the recolonizations (Figure 6.6). The average time to extinction was 25 years.

Because scenarios 4 - 7 represented further threats to the persistence of the marsh rabbit, these simulations were run both with the original life table and using the life history parameters in scenario #1(a) (survivorship was increased by 25% in all stages). When scenarios 4-7 were run using the actual life table survivorship estimates, 1 of the scenarios slightly increased the number of years before extinction and the other 3 scenarios hastened the amount of time before extinction (Table 6.6). Reducing migration 25% and

50% extended the number of years until the metapopulation went extinct from 28 years (for the basic simulation) to 30 years. A severe disease had the largest impact on the metapopulation persistence time; in this scenario the number of years to extinction was reduced to 3. A mild disease only decreased the persistence time by 8 years, producing a 20-year metapopulation persistence time. None of the hurricanes produced long-term changes in the persistence time of the metapopulation. A class 5 hurricane reduced the persistence time to 22 years and the class 4 and class 3 hurricanes reduced the time to 23 and 25 years, respectfully. None of the habitat loss scenarios (7a-c) had an effect on the overall persistence time of the metapopulation.

When the mortality in all of the stages was reduced by 25%, the scenarios had different effects on the persistence of the metapopulation. Scenario #4 examined the effect of a mild and a more severe disease had on S. p. hefneri (Figure 6.7). Although population numbers and the mean number of populations occupied was slightly lower than in 1(a), neither a mild or a severe disease appeared to have a large effect on population persistence.

When all of the Keys were simultaneously subjected to a hurricane (scenario #5), the effects on persistence were greater and persistence decreased with increasing hurricane impact (Figure 6.8). In all of the hurricane scenarios, population size and metapopulation occupancy decreased slightly over the 50 years.

Decreasing the amount of migration (scenario #6) did not alter the mean population size, but it did increase the amount of variance in population size (Figure 6.9). The number of occupied populations actually increased when there was only a 25% reduction in migration. When there was a 50% reduction, the number of occupied metapopulations was slightly below the results for unaltered migration rate results.

In scenario #7, patches were destroyed and removed from the simulation (Figure 6.10). When only the large site was removed (site #33), the population decreased to approximately 400 individuals (54 adults) and fluctuated slightly around this value. When 5 of the largest patches (including site #33) were removed, the population size declined nearly to extinction. Removal of the 10 smallest sites produced a similar effect, only the rate of the decline was faster.

Discussion

With its small body size, short life span, high reproductive output, and high habitat specificity, the Lower Keys marsh rabbit typifies the "good candidate" for a species that might exhibit classic metapopulation dynamics (Murphy et al. 1990, Thomas 1994). Over the time scale of this research (3 years), S. p. hefneri did appear to fit the pattern of a species that inhabited a patchy landscape yet was able to persist due to its dispersal ability. However,

if the results of the simulation model are correct, the Lower Keys marsh rabbit is doomed to extinction in the next 20-30 years.

Migration reduction, hurricanes, mild diseases, and habitat loss, will not significantly speed the decline of the Lower Keys marsh rabbit. A severe disease could cause the extinction of the entire metapopulation within 3 years.

Harrison (1991, 1994) suggested that most populations that appear to exist as stable metapopulations are actually on their way to extinction because most metapopulations do not exist in the "classic metapopulation" sense with patch recolonization exceeding patch extinction over long periods of time. Most of these doomed metapopulations are actually mainland-island metapopulations (where a large population sustains smaller populations) or non-equilibrium metapopulations (where there are insufficient movements between patches). The Lower Keys marsh rabbit differs because although it does appear to exist in the classic metapopulations structure in many ways, it is not lack of movements between populations that threatens its persistence.

Using the simulated management technique of decreasing cat predation (scenario #1), the model predicted that the population would fluctuate around a stable population size and would not experience extinction during the next 50 years. Other simulated management techniques such as recolonization and reducing vehicular mortalities were not successful in preventing extinction. This result indicates that the cat predation on the Lower Keys marsh rabbit is a

deterministic threat, and until it is removed no other management techniques will be successful.

Based on simulation, once the 25% increase in survivorship was implemented, only large-scale habitat destruction and a very severe hurricane were able to cause the rabbit's extinction. House cats have probably increased in the Lower Keys with increased human population during the past few decades. Extinction (or severe population declines) have been often attributed to exotic predators (e.g., domestic cat, Felis catus), although direct evidence is difficult to obtain.

Australia (Jones and Coman 1981), New Zealand (Fitzgerald and Karl 1979), and England (Churcher and Lawton 1989) have witnessed the decline in many species of small mammal, bird, and herpetofauna. It is believed that cats had a large role in the decline of these species. During recent attempts to reintroduce the ring-tailed possum (Pseudocheirus forbesi), cats killed nearly 75% of the animals (Anderson 1992). In Florida, cat density was negatively correlated with density of the endangered Anastasia Island Beach mouse (Frank 1993).

Model Validation

The conclusions made in this chapter are based on the assumption that the model accurately predicts the future persistence of S. p. hefneri. Proper

model validation requires that data be available to test the predictions of the model. Population abundance and metapopulation occupancy data are available for 2 years, but this is not long enough to perform a rigorous test of the model. In lieu of a validation Grant (1986) has proposed alternatives for evaluation a PVA model without actual data. He suggests that the scenarios used in the model be examined to determine if they accurately deal with the management issues to be addressed and if the results are expected. Then the parameters should be examined to determine their sensitivity to see if slight miscalculations could have severely biased the model. Sensitivity analysis found that none of the variables are extremely sensitive to the 25% and 50% increases.

The major assumption of the Lower Keys marsh rabbit PVA model is that population growth is not currently density-dependent. The data from which this assumption was made were collected at only 6 habitat patches on 2 keys. It is possible that population growth differs at other patches and at other keys. However, the fact that over two thirds of the populations on the Keys all appear to be far below carrying capacity indicates that a process other than density-dependence is in operation. It is possible that at higher survival rates, density dependence in terms of limiting fecundity or survival at densities above K might occur. The predicted population size of the 50% increase in marsh rabbit survival seen in Figure 6.4 indicates that the population would increase

far beyond the maximum carrying capacity for the habitat. It is likely that the Lower Keys marsh rabbit is currently at the low end of the sigmoidal curve that the logistic equation follows, and that increase survivorship would push the population size up the curve.

Assuming density-dependence was properly addressed in the model, there may also be questions about the realism of the scenarios. If it were possible to reduce the amount of cat predation in the Keys, it does not appear that predation from other predators would increase greatly. The only confirmed raccoon (Procyon lotor) predation occurred in the crook of a fence, where the raccoon cornered the rabbit, and this was also in an area with extremely high raccoon density due to the many open dumpsters in the area. Rattlesnakes (Crotalus adamanteus), the other predator in the system, are thought to exist at low densities in the Keys (Lazell 1989) and are often killed while crossing roads or when they enter people's yards.

Scenario #2, stopping mortality due to vehicles, would be difficult to achieve, but the incorporation of this mortality into the model was straightforward. Scenario #3, recolonization, was accurately depicted in the model if it is assumed that marsh rabbits would only be introduced to unoccupied sites on the major keys that are connected by US-1. Other empty areas of transition-zone habitat may exist on smaller islands off the major keys, and these islands are likely to be devoid of feral cats. If these keys were

included in the simulation, the life table for these areas might be dramatically different. This possibility suggests that a search for unoccupied habitat on the outer islands should be a high priority for future research (see Chapter 7).

The lack of an impact from a mild disease is highly predictable if one takes into account the rabbits sociality and the spatial structure of the transition-zone habitat. Marsh rabbits are mainly solitary in nature (Chapman et al. 1982), unlike their European relatives (Oryctolagus cuniculus) which are highly susceptible to disease. Marsh rabbits have little contact with any other rabbits from the time they are weaned to the time they mate. If the disease was spread through physical contact it only would affect a portion of the population. The disease would probably not spread as fast as it did in the simulation, unless it had another vector (e.g., ticks, mosquitoes).

The scenarios involving hurricanes might be less realistic. Each year in the Lower Keys there is a 10% chance of a hurricane (winds >74mph) making landfall (Chen and Gerber 1990). The chance that a hurricane hits the middle of the Lower Keys is probably <10%.

The results of the sixth scenario, decreasing migration, also should be treated with caution. It is difficult to predict how marsh rabbits will react if corridor habitat is altered. In the simulation, migration was reduced by 25% and 50%, indicating that rabbits without a good corridor habitat would not leave their patch. This may not be true; marsh rabbits might try and disperse

despite the lack of habitat and then perhaps face greater mortality without adequate food and cover. An experimental treatment of movements of Lower Keys marsh rabbits without corridor habitat is needed to clarify this process.

When migration was decreased by 25%, the overall abundance and number of patches occupied actually increased. When migration was cut by 50%, the overall population size appeared to increase, but the number of occupied patches was lower than with full migration or the 25% decline. So between the current amount of migration and a 25% reduction is the optimal dispersal rate for maintaining metapopulation persistence.

Results from the last scenario provide insight into the importance of individual patches to the overall metapopulation persistence. When mortality was reduced by 25%, the elimination of the largest site simply decreased the overall number of rabbits and the number of patches occupied. The destruction of 5 large and 10 small patches lead to extinction. These last 2 scenarios lead to extinction at nearly the same rate despite the fact that the 5 largest patches contain 128.1 ha of habitat while the 10 small contain less than 10 ha. The importance of a patch to the overall metapopulation persistence is more than just the amount of area is encompasses. Thus, further habitat loss of small, individual patches is a severe threat to the subspecies' persistence.

Minimum Viable Population, Area, and Number of Patches

Using the current Leslie matrix values, it does not seem that there is any minimum population size (Soulé 1980) that could reasonably be called viable for even short-term persistence. With the 25% increase in survivorship, the effective population size (N_e) varied around 167 (or 334 adults if a 1:1 sex ratio is assumed). This is above the hypothesized minimum level of 50 to avoid inbreeding problems, but below the level of 500 individuals, which is the level necessary to maintain genetic diversity (see Lande and Barrowclough 1987).

Minimum viable area seems less appropriate in this situation than minimum number of patches. The number of occupied patches was seen to be more important than the size of the patches, although the connectivity of the patches might also be important. Judging from the results of scenario #7 (habitat loss), this minimum number of patches for metapopulation persistence is between 20 and 30 patches spread over at least 3 keys.

These results suggest that although S. p. hefneri is probably currently moving toward extinction, an increase in survivorship might cause the subspecies to persist in a "classic - equilibrium" metapopulation. For the Lower Keys marsh rabbit, the metapopulation "paradigm" can form a useful framework from which to build recovery actions.

Table 6.1--Parameters used by stage (1 = nestling, 2 = juvenile, 3 = subadult, 4 = adult1, 5 = adult2) for RAMAS simulations involving marsh rabbit populations under different scenarios. Reproductive rates were held constant for all scenarios.

Scenario	Mortality					Catastrophe					Migration				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Basic (exponential)	0.28	0.75	0.67	0.52	0.10	0	0	0	0	0	0	0	0.75	0	0
#1a. Predator control leads to 25% less mortality.	0.42	0.81	0.75	0.64	0.33	0	0	0	0	0	0	0	0.75	0	0
#1b. 50% less mortality.	0.60	0.87	0.83	0.76	0.53	0	0	0	0	0	0	0	0.75	0	0
#2. All vehicular deaths are avoided.	0.28	0.75	0.75	0.60	0.10	0	0	0	0	0	0	0	0.75	0	0
#3. Rabbits are reintroduced to all vacant patches.	0.28	0.75	0.67	0.52	0.10	0	0	0	0	0	0	0	0.75	0	0
All of the following scenarios are conducted assuming that mortality for all stages has been reduced by 25%.															
#4a. A disease causing some fatalities is spread through the keys. The effect is local, but each patch has a 95% chance of getting infected each year.	0.42	0.81	0.75	0.64	0.33	0.25	0	0	0.25	0.25	0	0	0.75	0	0
#4b. More severe disease.	0.42	0.81	0.75	0.64	0.33	0.95	0	0	0.95	0.95	0	0	0.75	0	0

Table 6.1 --(Continued.)

Scenario	Mortality					Catastrophe					Migration				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
#5a. A class 3 hurricane has a 10% chance of hitting the keys.	0.42	0.81	0.75	0.64	0.33	0.75	0.50	0.25	0.25	0.25	0	0	0.75	0	
#5b. Class 4.	0.42	0.81	0.75	0.64	0.33	0.95	0.75	0.50	0.50	0.50	0	0	0.75	0	0
#5c. Class 5.	0.42	0.81	0.75	0.64	0.33	0.99	0.90	0.75	0.75	0.75	0	0	0.75	0	0
#6a. Corridor habitat is destroyed and decreases migration by 25%.	0.42	0.81	0.75	0.64	0.33	0	0	0	0	0	0	0	0.56	0	0
#6b. migration decreases by 50%.	0.42	0.81	0.75	0.64	0.33	0	0	0	0	0	0	0	0.38	0	0
#7. The largest patch (site #33) is destroyed.															
#7b. The five largest patches are destroyed.	0.42	0.81	0.75	0.64	0.33	1	1	1	1	1	0	0	0.75	0	0
#7c. The 10 smallest patches are destroyed.	0.42	0.81	0.75	0.64	0.33	1	1	1	1	1	0	0	0.75	0	0

Table 6.2--Mean number of pellets produced by captive marsh rabbits (Sylvilagus palustris hefneri) during a 24-hour period. Equal numbers of adult males and females were used each session.

Session	Date	Number of rabbits	Mean number of pellets	SE
1	Feb 1991	4	171.0	7.43
2	Jul 1991	4	120.0	10.61
3	Nov 1991	4	132.0	13.37
4	Mar 1992	4	134.0	17.20
5	Jul 1992	4	104.8	10.50
6	Nov 1992	4	120.8	14.22
7	Mar 1993	4	107.3	10.72
8	Jul 1993	4	103.8	7.13

Table 6.3--Fitting the frequency distribution of the number of pellets per sampling unit to the Poisson model for sample units using 0.5-m and 1-m radii. The degree of correspondence is measured using a chi-square test. A significant result indicates that the distribution is not random.

	0.5-m radius			1.0-m radius		
Site	Chi-square	d.f.	$P \leq 0.05$	Chi-square	d.f.	$P \leq 0.05$
1	12.46	6	no	86.48	6	yes
2	3.88	2	no	7.48	2	yes
3	0.07	1	no	0.11	1	no
4	16.66	9	no	36.22	10	yes
5	0	0		0	0	
6	2.70	3	no	7.18	2	yes
7	3.52	9	no	3.88	6	no
8	17.73	6	yes	101.31	6	yes
9	24.70	9	yes	26.79	9	yes
10	31.76	7	yes	37.68	7	yes
11	34.71	8	yes	61.58	8	yes
12	7.47	4	no	12.35	9	yes
13	60.64	9	yes	77.73	9	yes
14	0.84	4	no	8.96	3	yes

Table 6.4--Number and proportion of habitat patches that existed above and below carrying capacity (K). The total estimated number of Lower Keys marsh rabbits (Sylvilagus palustris hefneri) was calculated for the 39 sites where density estimates were conducted and was averaged over the 8 sessions. This average was compared to K.

% larger or smaller	Number of sites in this category	Proportion of sites
0-19% larger	4	10.0%
20-39% larger	3	7.5%
40-59% larger	2	5.0%
60-79% larger	2	5.0%
80-100% larger	0	0.0%
Total larger	11	27.5%
0-19% smaller	4	10.0%
20-39% smaller	0	0.0%
40-59% smaller	1	2.5%
60-79% smaller	7	17.5%
80-100% smaller	15	37.5%
Total smaller	28	67.5%

Table 6.5--Sensitivity analysis for population parameters. Each of the parameters used in the model was increased by 25% and 50% to see how sensitive these parameters are to changes in value or errors in estimation.

Simulation	Abunance (SE)	Number of Populations (SE)	Years to Extinction - 1 SE	Mean	+ 1SE
25% more nestlings	180.3 (25.6)	11.6 (0.9)	39	>50*	>50
50% more nestlings	765.8 (17.2)	26.8 (0.5)	>50	>50	>50
25% more juveniles	105.1 (31.8)	16.7 (1.3)	26	38	46
50% more juveniles	344.2 (34.2)	18.1 (1.2)	32	49	>50
25% more subadults	154.1 (37.3)	9.0 (1.4)	28	39	>50
50% more subadults	169.3 (37.9)	10.1 (1.4)	28	45	49
25% more adult 1	205.3 (28.1)	23.5 (0.8)	>50	>50	>50
50% more adult 1	239.6 (32.6)	24.5 (0.7)	>50	>50	>50
25% more adult 2	173.1 (34.7)	23.1 (0.8)	>50	>50	>50
50% more adult 2	301.5 (34.8)	23.7 (0.8)	>50	>50	>50
25% more reproduction	176.2 (38.3)	10.2 (1.4)	30	45	>50
50% more reproduction	275.3 (42.5)	14.9 (1.3)	41	>50	>50

*>50 indicates that the population size did not reach zero during the 50 year simulation.

Table 6.6.--The number of years until the Lower Keys marsh rabbit (Sylvilagus palustris hefneri) goes extinct as predicted by the PVA simulation model under 4 different scenarios. The mortality rate for each stage was taken from the original life table.

Scenario	Number of years until extinction		
	-1 SE	Average	+1 SE
Basic	21	28	33
4a. Mild disease	15	20	25
4b. Severe disease	2	3	4
5a. Class 3 hurricane	22	25	28
5b. Class 4 hurricane	21	23	25
5c. Class 5 hurricane	20	22	24
6a. Reduce migration (25%)	21	30	34
6b. Reduce migration (50%)	19	30	34
7a. Destroy largest patch	20	27	32
7b. Destroy 5 largest patches	21	27	33
7c. Destroy 10 smallest patches	21	28	33

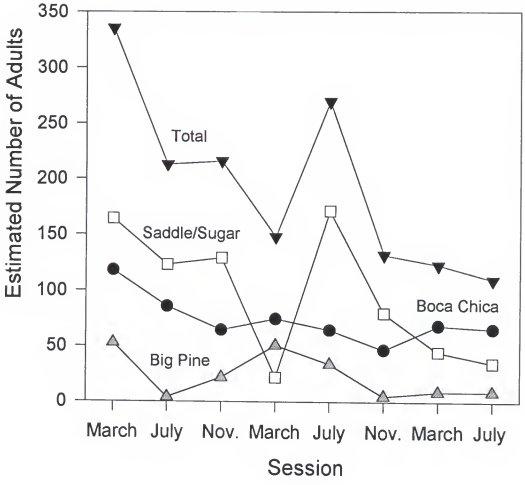


Figure 6.1--The number of adult Lower Keys marsh rabbits (Sylvilagus palustris hefneri) estimated during the 8 pellet-counting sessions (March 1991 - July 1993), by Key group (see Appendix A).

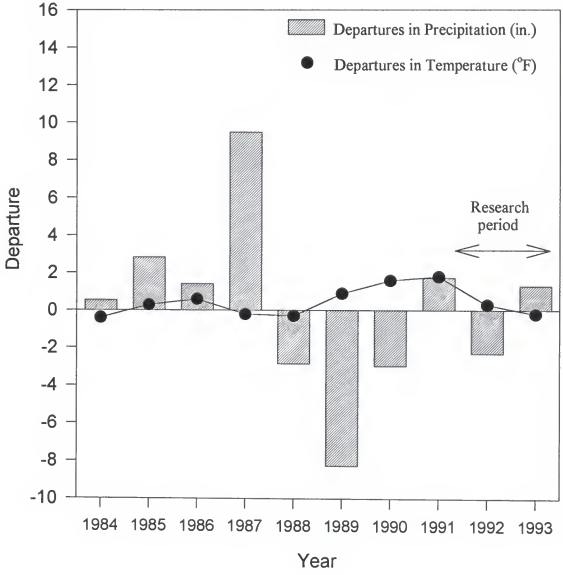
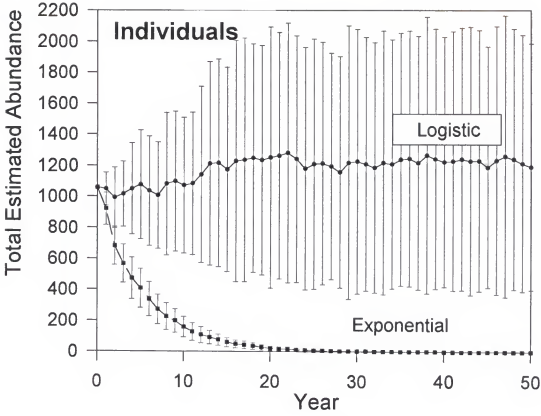


Figure 6.2--Departures in precipitation and temperature during the past 10 years, using the past 30 years as a base.

Figure 6.3--Predictions (and error bars) of the population viability analysis model for the Lower Keys marsh rabbit (Sylvilagus palustris hefneri) using density-dependent population growth (logistic equation) and density-independent growth (exponential equation).


Individuals
Total Estimated Abundance
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
0
Logistic
Exponential
0
10
20
30
40
50
Year

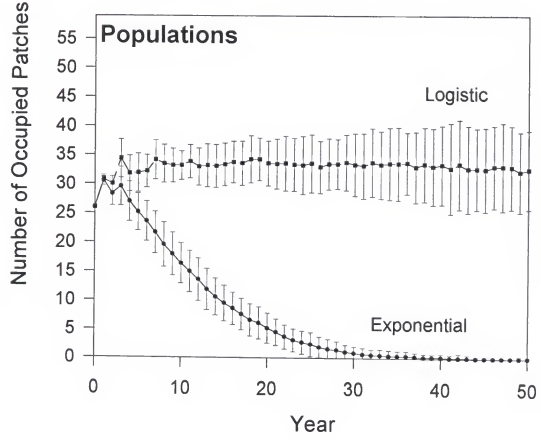
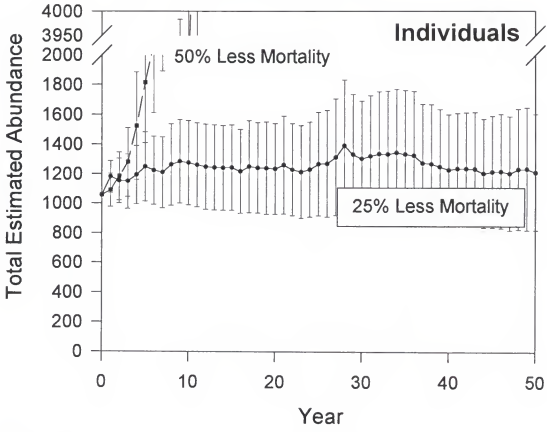

Populations
Number of Occupied Patches
55
50
45
40
35
30
25
20
15
10
5
0
Logistic
Exponential
0
10
20
30
40
50
Year

Figure 6.4--Results of Scenario #1 (Predator control) of the Lower Keys marsh rabbit (Sylvilagus palustris hefneri) PVA model, where survivorship was increased in all stages by 25% and 50%.


Individuals
50% Less Mortality
25% Less Mortality
Total Estimated Abundance
4000
3950
2000
1800
1600
1400
1200
1000
800
600
400
200
0
0
10
20
30
40
50
Year

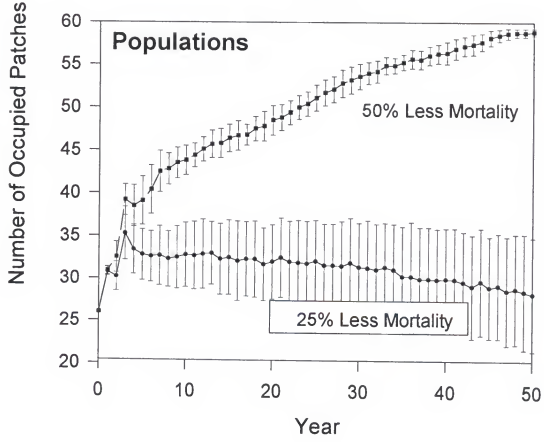
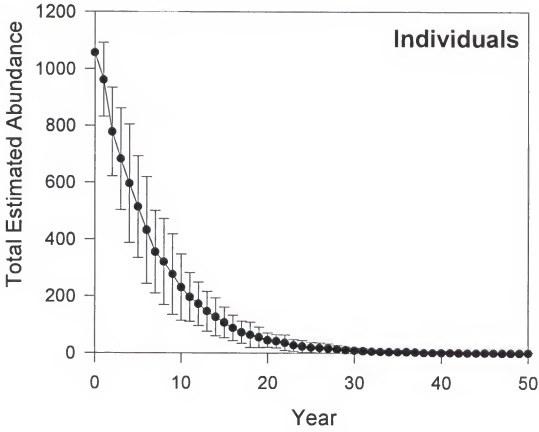

Populations
50% Less Mortality
25% Less Mortality
Number of Occupied Patches
60
55
50
45
40
35
30
25
20
0
10
20
30
40
50
Year

Figure 6.5--Results of Scenario #2 (all vehicular deaths are avoided) of the Lower Keys marsh rabbit (Sylvilagus palustris hefneri) PVA model, where survivorship was increased in the subadult stage by 25% and 10% in the adult1 stage.


Individuals
Total Estimated Abundance
1200
1000
800
600
400
200
0
0
10
20
30
40
50
Year

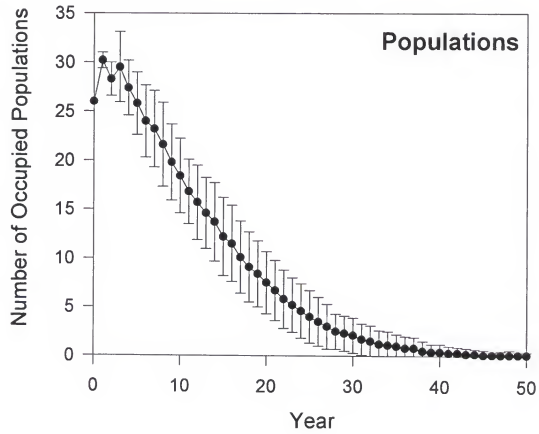
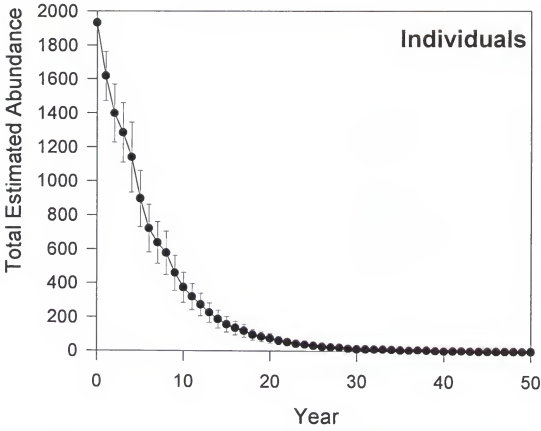

Populations
Number of Occupied Populations
35
30
25
20
15
10
5
0
0
10
20
30
40
50
Year

Figure 6.6--Results of Scenario #3 of the Lower Keys marsh rabbit (Sylvilagus palustris hefneri) PVA model, where marsh rabbits were reintroduced to all vacant patches.


Individuals
Total Estimated Abundance
2000
1800
1600
1400
1200
1000
800
600
400
200
0
0
10
20
30
40
50
Year

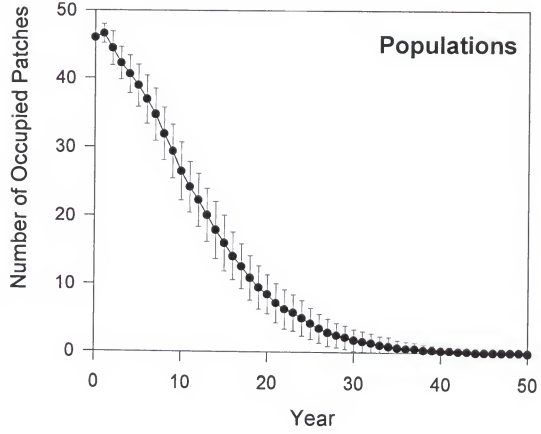
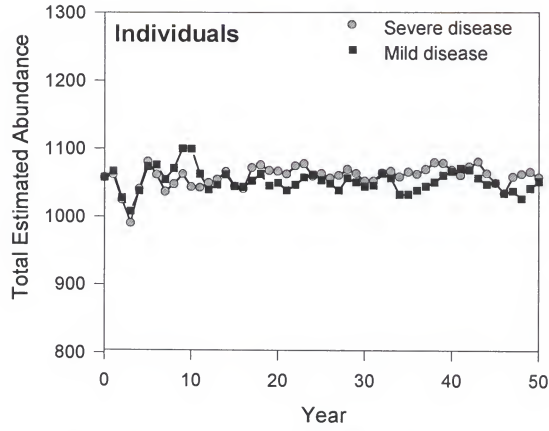

Populations
Number of Occupied Patches
50
40
30
20
10
0
0
10
20
30
40
50
Year

Figure 6.7--Results of Scenario #4 of the Lower Keys marsh rabbit (Sylvilagus palustris hefneri) PVA model. In the mild disease simulation, 25% of all nestling and adult rabbits died at infected patches and each patch had a 75% chance of getting infected each year. In the severe disease simulation, 75% of all nestling and adult rabbits died.


Individuals
Severe disease
Mild disease
Total Estimated Abundance
1300
1200
1100
1000
900
800
0
10
20
30
40
50
Year

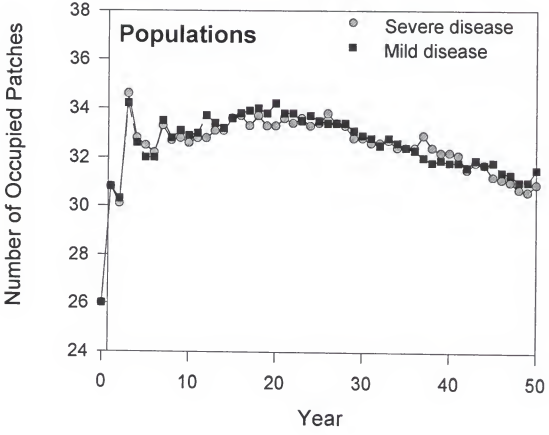
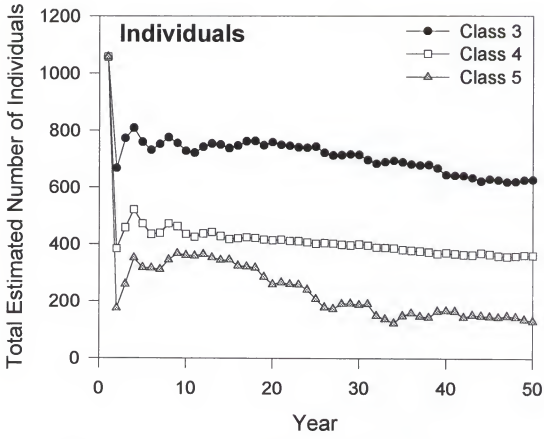

Populations
Severe disease
Mild disease
Number of Occupied Patches
38
36
34
32
30
28
26
24
0
10
20
30
40
50
Year

Figure 6.8--Results of Scenario #5 of the Lower Keys marsh rabbit (Sylvilagus palustris hefneri) PVA model. The effects of a hurricane kill rabbits in each stage, with the youngest rabbits being the most likely to die. Class 3 produces the lowest mortality and class 5 the highest.


Individuals
Class 3
Class 4
Class 5
Total Estimated Number of Individuals
1200
1000
800
600
400
200
0
0
10
20
30
40
50
Year

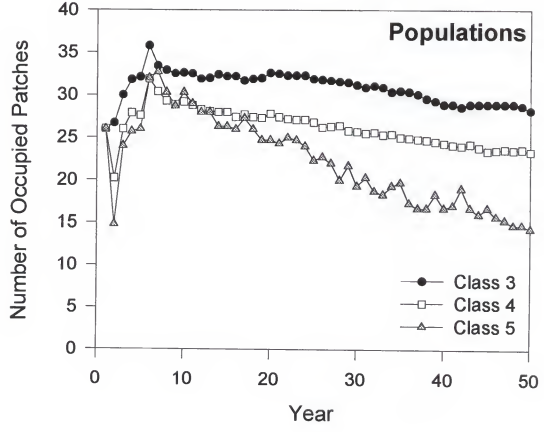
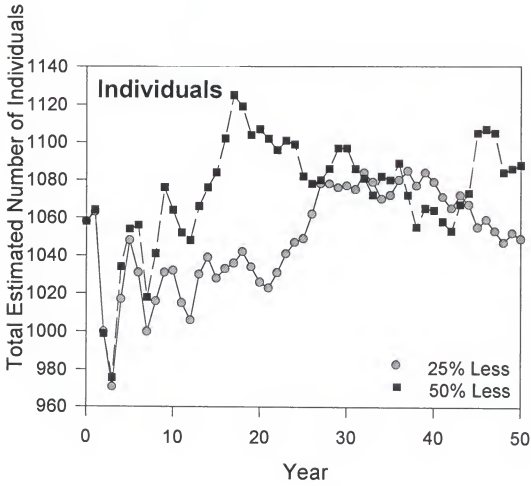

Populations
Number of Occupied Patches
40
35
30
25
20
15
10
5
0
Class 3
Class 4
Class 5
0
10
20
30
40
50
Year

Figure 6.9--Results of Scenario #6 of the Lower Keys marsh rabbit (Sylvilagus palustris hefneri) PVA model. Corridor habitat is destroyed, causing a 25% and 50% reduction in dispersing individuals.


Individuals
Total Estimated Number of Individuals
1140
1120
1100
1080
1060
1040
1020
1000
980
960
0
10
20
30
40
50
Year
25% Less
50% Less

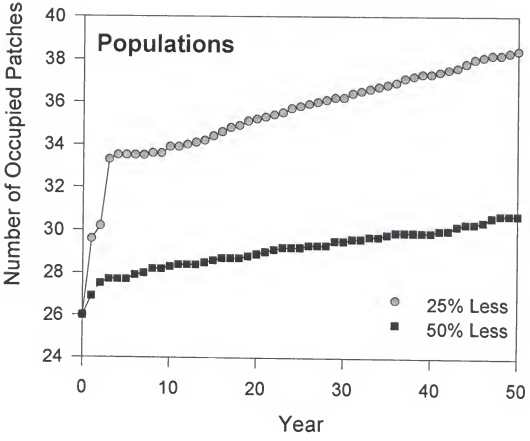
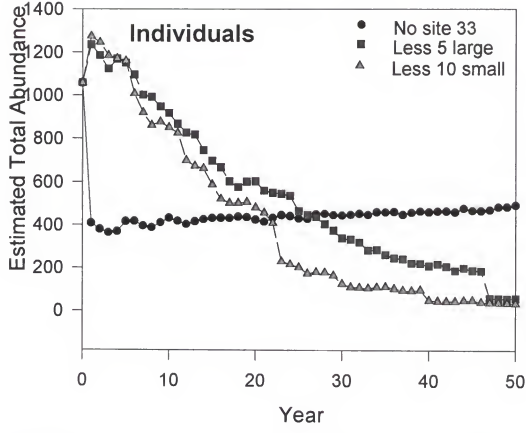
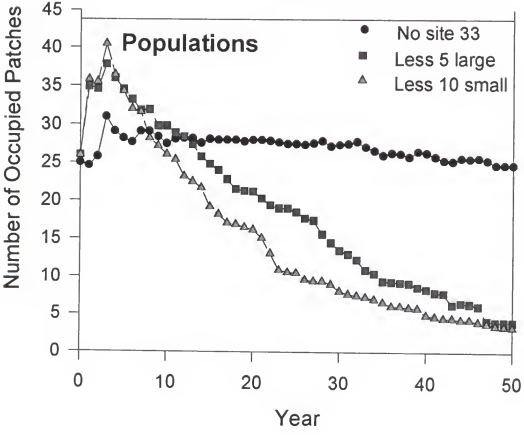

Populations
Number of Occupied Patches
40
38
36
34
32
30
28
26
24
0
10
20
30
40
50
Year
25% Less
50% Less

Figure 6.10--Results of Scenario #7 of the Lower Keys marsh rabbit (Sylvilagus palustris hefneri) PVA model. In the first simulation the largest patch (#33) is destroyed, in the second the 5 largest patches are destroyed, and in the last simulation 10 of the smallest patches are destroyed.


Individuals
No site 33
Less 5 large
Less 10 small
Estimated Total Abundance
1400
1200
1000
800
600
400
200
0
0
10
20
30
40
50
Year


Populations
No site 33
Less 5 large
Less 10 small
Number of Occupied Patches
45
40
35
30
25
20
15
10
5
0
0
10
20
30
40
50
Year

CHAPTER 7
CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

Population Viability Analysis (PVA) and Metapopulation Dynamics

Recently, the political and legal battle over the spotted owl (Strix occidentalis occidentalis) and other listed species have spurred debate about the uses of PVA (Boyce 1992, Harrison 1994). A PVA model can have vastly different outcomes depending on the parameters and algorithms used, and therefore might not be legally defensible. Because of these legal problems, Harrison (1994) suggests that we should seek "sensible" alternatives to PVA such as "comparing the abundances of species of concern in forests (or other habitats) of varying degrees of fragmentation". However, it is difficult to see how correlative studies will exceed the power of a good PVA and how this will solve the legal problems associated with endangered species.

At its worst, conducting a PVA can demonstrate where more data is needed, and the results can be interpreted knowing the assumptions of the model. This will provide more information than simple estimates of minimum viable population size (MVP) and extinction probabilities associated with MVP (Boyce 1992).

At its best, a PVA can help understand how a species interacts with its environment and define the processes that are most important in persistence. Combined with the scientific method, a PVA can be used in hypothesis testing about the cause of the species' decline and how different management techniques can halt this decline. These techniques can be applied at small scales, and then the results extended throughout the species using a PVA model, but appropriate validation of the model should be conducted at a variety of locations.

Recently, several population simulation models (VORTEX, Lacy 1993, RAMAS, Akçakaya 1994) have been extended to include spatial structure in their analysis of population viability. Most endangered species exist in highly fragmented habitats and the spatial structure of the PVA model should include the interchange among habitat fragments. If habitat patches are highly independent of each other with little exchange between patches, then it may be best to model each patch independently. If movement between patches is so great that the rabbits exist as a single population, then the spatial structure of the habitat patches is not an important feature to be included in the model. However, when the species exists in a metapopulation, the spatial structure of the patches should be included. In VORTEX and RAMAS, inter-population movements are incorporated into these models based on measured dispersal information or based solely on the spatial structure of the metapopulation.

Using spatially explicit models, the extinction and recolonization of individual patches (metapopulation dynamics) can be simulated. Metapopulations are affected by the same threats as single individual populations, in addition to threats that occur at the metapopulation level. PVA models can assess the chance of local extinctions and the chance of metapopulation extinction.

Harrison (1991) has postulated that most endangered species that exist in metapopulations are actually fragmented populations on the decline, as is the case of the spotted owl (Strix occidentalis occidentalis; LaHaye et al. 1994) and the Lower Keys marsh rabbit (Sylvilagus palustris hefneri). The transition-zone marsh habitat of the Lower Keys marsh rabbit once existed as a concentric ring located on each key between the mangroves and the upland hardwood hammocks. Development has broken the ring, creating a patchy distribution of transition zone habitat.

Few metapopulations of endangered species persist in the structure predicted by Levins (1969, 1970) and Hanski and Gilpin (1991), where the number of recolonized patches is greater or equal to the number of patches that go extinct. Most endangered species occur in a fragmented landscape because an intact landscape is not available, and creation of one is not possible. Metapopulation dynamics and PVA can be used to determine what

management techniques are necessary to allow the endangered species to persist as a metapopulation.

Management for Recovery of the Lower Keys Marsh Rabbit

A detailed recovery plan has been written for S. p. hefneri (United States Fish and Wildlife Service 1993). Recommendations made in the recovery plan are incorporated with the results of the PVA model presented in this manuscript.

Primary Recovery Actions

If current mortality rates persist, it is likely that the Lower Keys marsh rabbit will go extinct during the next 20-30 years. The first goal in the recovery efforts should be increasing survivorship in all stages, but especially in the nestling and adult stages.

The main source of juvenile to adult mortality, and probably nestling mortality, is domesticated cats (Felis catus) (Chapter 3). Reducing mortality by cats is particularly difficult because domestic cats can be difficult to catch, poisoning or shooting cats in suburban areas could incite public outrage, and because many of the cats in the rabbit's habitat are free-ranging house cats.

The best method of cat control may be a combination of long-term public education and trapping in marsh rabbit habitat. A long-term public

education program may help by increasing the number of pets that are sterilized, decreasing the number of cats that are abandoned, and decreasing the number of pet cats that are allowed to roam outdoors. Changing the public's opinion on their cat's outdoor-time through education has not generally been successful in other areas (Proulx 1988).

Trapping the cats in marsh rabbit habitat and bringing cats to the Animal Control Pound, might further reinforce cat owners to keep their cats indoors. Other actions might include experimenting with cat bells to determine if they work in reducing the cat's hunting ability. Cat-proof fencing is not feasible in most of the areas because most of the habitat exists in small patches and the larger patches are shared with a suite of native species that would be negatively impacted by the fences.

As a prerequisite to reduce overall marsh rabbit mortality and to prevent further habitat loss, marsh rabbit habitat must be purchased and managed. A cat trapping program will be easier to implement if the land is owned by the state or federal government or an environmental non-government agency. As the results of scenario #7 (habitat loss) of the PVA model demonstrated, even small habitat patches are important to the overall persistence of S. p. hefneri. A complete listing of land parcels for acquisition is given in the Lower Keys marsh rabbit Recovery Plan (United States Fish and Wildlife Service 1993). The largest parcel is covered by a Conservation and Recreative Lands (CARL)

proposal (#910130-44-1, Hammocks of the Lower Keys). This CARL proposal is currently ranked at number 2 in the State of Florida and is available for funding.

Because it will be difficult to lower the mortality from cats and to acquire marsh rabbit habitat, additional subpopulations of marsh rabbits should be founded in areas not occupied by domestic cats. A thorough survey of the federally-owned back-country islands of the National Key Deer Refuge should be conducted and marsh rabbits should be reintroduced to suitable islands. Reintroduction to areas on Keys connected by US-1 should occur after the number of cats has been reduced.

Secondary Recovery Actions

Even protected areas require habitat management to maintain the maximum marsh rabbit carrying capacity of the habitat. The Lower Keys marsh rabbit appears to rely on dense ground cover, particularly in the mid- and high marsh (Chapter 5). Potential threats to this vegetation included exotic vegetation, off-road vehicle (ORV) use, mowing, and trash dumping.

Australian pine (Casurina equisetifolia) and Brazilian pepper (Shinus terebinthefolius) are rapid non-native colonizers in the transition zone that inhibit or deter understory growth. These trees are particularly abundant on Boca Chica Key, but are present on all of the Keys. Girdling trees with

applications of GARLON has been found to be a fast, effective method of killing these exotics.

Off-road vehicle traffic (ORV) compacts soil, destroys vegetation and increases erosion. Off-road vehicle traffic through marsh rabbit habitat can be stopped by preventing access to habitats from the road. Local education programs involving law enforcement and military police officers have been helpful in preventing ORV use of wetlands. Deterring ORV use of wetlands also decreases the amount of illegal dumping.

Restoration of vegetation in areas that have been badly damaged by ORV use, dumping, or other land uses may be needed at some areas. Restoration, although costly, may increase the total amount of habitat available to the marsh rabbit. A trial restoration project has been initiated at site #10 on Boca Chica.

In addition to protecting habitat, protection of marsh rabbit dispersal corridors is also important in preserving the subspecies. Marsh rabbits will move through any habitat that is not disturbed (Chapter 4). Future development plans in the Keys should be evaluated for their impact on corridor habitat.

Although cats are the main predator of the marsh rabbit, reducing other sources of mortality may significantly increase the marsh rabbit population. Raccoons (Procyon lotor) are not as great of a threat to the persistence of S. p.

hefneri (Chapter 3) as cats, but raccoon numbers may be increased locally in areas with open dumpsters. Providing top-closing lid dumpsters might decrease the numbers of raccoons. Other native species such as Bald Eagles (Haliaeetus leucocephalus) and Rattlesnakes (Crotalus adamanteus) and exotic species (e.g. dogs, Canis familiaris) are not seen as being a threat to Lower Keys marsh rabbit's survival.

A significant number of rabbits are killed by vehicles (Chapter 3). While it is not likely to prevent all of these mortalities, the number of deaths might be reduced if speed limits were enforced. The most important time to enforce speedlimits is from dusk to dawn, when the rabbits are most active.

Although undocumented, there may be additional sources of mortality in the nestling stage. At this stage, rabbits are extremely altricial and perhaps more susceptible to some types of predation than older rabbits. Fire, while fairly rare in the transition zone, might have a impact on younger rabbits that are incapable of escaping. Overall, fire probably has a positive effect on the rabbit because of its effect on understory vegetation.

Mowing, while not having a large impact on older rabbits that can run away, might have a large effect on nestlings. Mowing may additionally change the composition and diversity of the plants in the marsh rabbit habitat.

Red imported fire ants (Solenopsis invicta) have recently colonized the Keys and are abundant in some of the transition zone areas (Forys pers. obs.).

These fire ants are attracted to the mucous found on young rabbits and were a major source of mortality in Eastern cottontail young (Sylvilagus floridanus; Hill 1969, 1972).

Future Research

Annual population monitoring will be important in validating the PVA model and determining the effectiveness of management techniques. The results of the PVA simulation (Chapter 6) showed that the number of occupied patches was similar to the total number of rabbits. Censusing areas for presence or absence of marsh rabbit pellets is a fast and efficient method of determining patch occupancy. Presence/absence data can be obtained for a site in less than one hour. Using the methods reported in this study, pellet counting for abundances uses 4 hours per site and live-trapping takes 20 hours for each site.

Further research on the possibility of reintroducing Lower Keys marsh rabbits also should be explored. Potential reintroduction sites first need to be evaluated for habitat suitability and then the ability of rabbits to interact with the greater metapopulation should be measured. Routine translocations of marsh rabbits might be necessary to provide genetic interchange with the "mainland" Keys populations.

Other future research should be aimed at decevising means of decreasing the mortality rate of the marsh rabbits. With all research projects small experimental treatments should be applied first, their effects incorporated into the PVA model, and then successful management techniques should be used throughout the Lower Keys.

APPENDIX A
DESCRIPTIVE INFORMATION ABOUT THE HABITAT PATCHES AND MAPS

Each transition zone site in the Lower Keys of Florida is listed by the Key it occurs on, the area of the habitat patch, the ownership, and whether the patch was included in the density estimates. Maps with each site located by number follow this appendix.

Key	Site #	Area	Ownership*	Density
Boca Chica	1	1.05	USN	Yes
Boca Chica	2	1.22	USN	Yes
Boca Chica	3	1.62	USN	Yes
Boca Chica	4	2.92	USN	Yes
Boca Chica	5	2.43	USN	Yes
Boca Chica	6	2.75	USN	Yes
Boca Chica	7	3.89	USN	Yes
Boca Chica	8	3.90	USN	Yes
Boca Chica	9	4.86	USN	Yes
Boca Chica	10	2.27	USN	Yes
Boca Chica	11	5.18	USN	Yes
Boca Chica	12	2.33	USN	Yes
Boca Chica	13	3.40	USN	Yes
Boca Chica	14	5.83	USN	Yes
Boca Chica	15	1.15	USN	Yes
Boca Chica	16	0.69	USN	Yes
Boca Chica	17	1.04	USN	Yes
Boca Chica	18	0.55	USN	No
Boca Chica	19	1.50	USN	No
Boca Chica	20	1.00	USN	No
Boca Chica	21	3.00	USN	No
Boca Chica	22	0.30	USN	No
Boca Chica	23	0.50	USN	No
Boca Chica	24	0.50	USN	No
Boca Chica	25	1.56	?	Yes
Boca Chica	26	0.45	USN	No
Boca Chica	27	0.30	?	No

Key	Site #	Area	Ownership*	Density
Saddlebunch	28	3.50	USFWS	Yes
Saddlebunch	29	2.50	USN	Yes
Saddlebunch	30	0.78	USN	Yes
Sugarloaf	31	1.00	P	Yes
Sugarloaf	32	4.00	P	Yes
Sugarloaf	33	31.50	P	Yes
Sugarloaf	34	2.30	P	Yes
Sugarloaf	35	0.86	P	No
Sugarloaf	36	0.57	P	No
N. Saddlebunch	37	0.58	Monroe	No
N. Saddlebunch	38	0.50	P	No
N. Saddlebunch	39	0.55	P	No
N. Saddlebunch	40	0.69	P	No
Cudjoe	41	2.60	P	Yes
Cudjoe	42	3.90	Air	Yes
Cudjoe	43	5.50	P	Yes
Summerland	44	2.34	P	Yes
Ramrod	45	3.90	P	Yes
Middle Torch	46	1.00	USFWS	No
Middle Torch	47	1.73	USFWS	No
Big Torch	48	0.50	P	No
Big Torch	49	0.88	USFWS	No
Big Torch	50	1.44	P	Yes
Little Torch	51	3.00	TNC	Yes
Big Pine	52	4.45	USFWS	No
Big Pine	53	19.50	USFWS	Yes
Big Pine	54	43.70	SFWMD	Yes
Big Pine	55	27.60	SFWMD	Yes
Big Pine	56	1.10	P	Yes
Big Pine	57	1.00	P	Yes
Big Pine	58	2.93	USFWS	Yes
Noname	59	1.50	USFWS	Yes

*USN - United States Navy, P = privately owned, USFWS = United States Fish and Wildlife Service, Monroe = Monroe County, Air = United States Airforce, TNC = The Nature Conservancy.

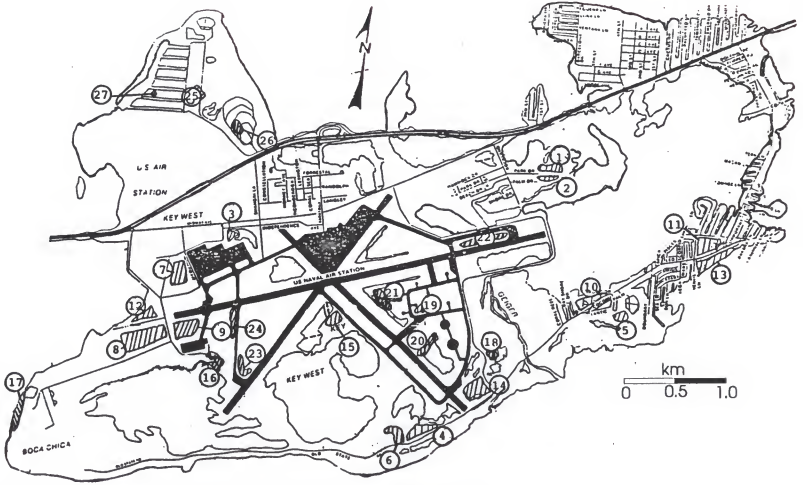


Figure A.1--A map of Boca Chica Key. The habitat patches used in the study are numbered.

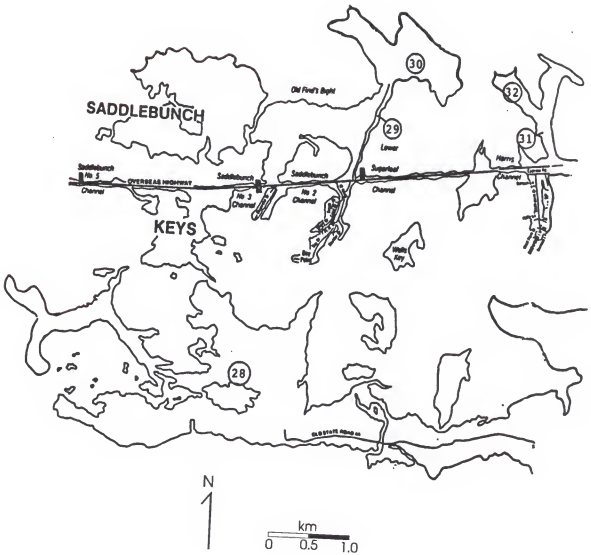


Figure A.2--A map of Saddlebuch and Lower Sugarloaf Keys. The habitat patches used in the study are numbered.

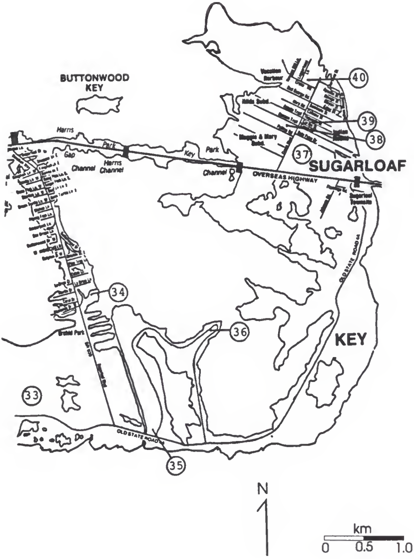


Figure A.3--A map of Sugarloaf Key. The habitat patches used in the study are numbered.

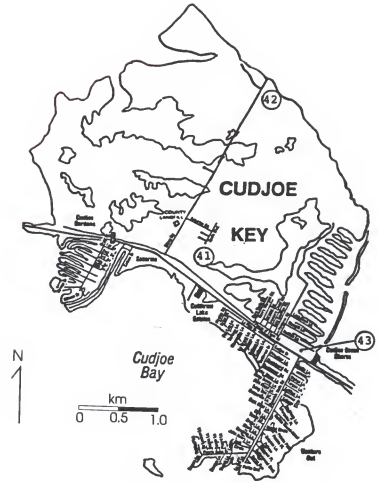


Figure A.4--A map of Cudjoe Key. The habitat patches used in the study are numbered.

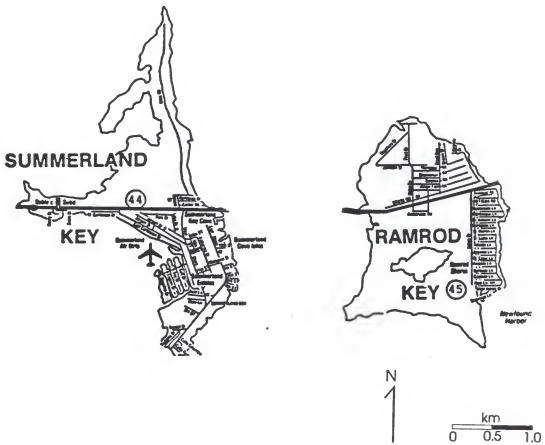


Figure A.5--A map of Summerland and Ramrod Keys. The habitat patches used in the study are numbered.

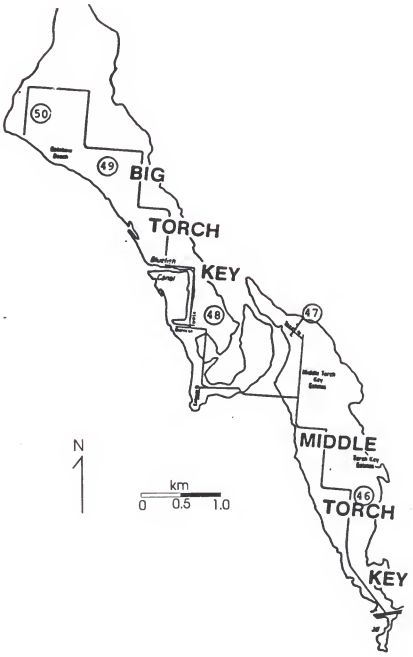


Figure A.6--A map of Big Torch and Middle Torch Keys. The habitat patches used in the study are numbered.

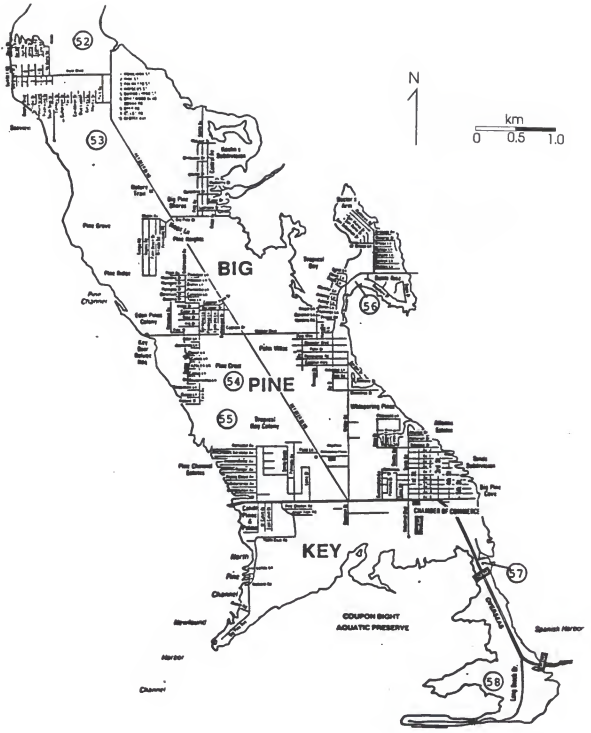


Figure A.7--A map of Big Pine Key. The habitat patches used in the study are numbered.

Figure A.8--A map of Noname Key. The habitat patches used in the study are numbered.

APPENDIX B
VARIABLES USED IN THE DISCRIMINANT FUNCTION ANALYSIS

Table B.1--The variables used in the descirminant function analysis.

site	code	%gcover	%ccover	H'	hgt	%bf	%clump	area	dwat	dpeop	isol
1	2	71	30	2.05	42.1	3	46	1.05	1	270	40
2	2	64	28	2.17	34.1	2	37	1.22	108	90	40
3	1	44	19	1.24	20.2	0	4	1.62	90	540	376
4	2	77	25	1.44	15.0	15	20	2.92	1	2700	166
5	1	35	5	0.93	10.0	2	5	2.43	18	660	153
6	1	70	35	1.76	15.0	7	2	2.75	1	2880	100
7	2	72	19	1.14	18.4	1	27	3.89	135	1170	213
8	2	57	8	2.02	22.9	20	19	3.9	135	1710	124
9	2	78	20	1.25	19.4	2	30	4.86	180	1476	163
10	2	83	6	1.04	41.5	3	57	1.27	90	900	333
11	2	58	9	1.21	42.5	20	18	5.18	90	1	51
12	2	45	4	1.27	20.4	3	25	2.33	135	1710	124
13	2	55	8	1.33	40.2	15	32	3.40	98	1	51
14	2	60	6	1.31	28.5	3	35	5.83	136	1836	190
15	1	32	20	0.67	19.0	4	13	1.15	1	720	318
16	1	47	8	1.28	15.9	29	3	0.69	1	1680	153
17	1	35	14	1.49	12.1	7	2	1.04	1	2160	628
18	1	70	10	1.55	20.5	33	4	0.55	60	600	168
19	1	62	3	0.96	18.9	2	15	1.50	110	550	280
20	1	51	13	1.15	17.8	5	10	1.00	1	575	259
21	2	52	12	1.45	24.6	7	22	3.00	1	470	232
22	1	51	5	1.32	22.0	7	15	0.30	90	480	211
23	1	41	3	1.27	21.0	5	9	0.50	130	870	226
24	1	46	15	1.7	26.2	4	7	0.50	250	540	251
25	2	61	19	1.81	13.9	0	52	1.56	1	1500	353
26	2	68	25	1.2	36.6	12	36	0.45	150	1100	405
27	1	55	19	0.91	29.6	2	16	0.30	10	1560	483
28	1	93	18	1.56	9.1	10	11	3.50	110	6000	2124
29	1	50	9	1.42	20.3	1	17	0.78	500	2000	403
30	2	98	12	1.85	7.2	2	46	2.50	100	3000	472

Table B.1--Continued.

site	code	%gcover	%ccover	H'	hgt	%bf	%clump	area	dwat	dpeop	isol
31	2	70	4	1.6	6.5	7	30	1.0	1	300	383
32	2	56	5	1.38	17.0	10	39	4.0	100	1000	383
33	2	98	5	1.12	62.0	8	87	31.50	1	2000	1800
34	1	37	13	1.57	15.0	4	10	2.30	1	1	832
35	1	60.4	12	1.84	15.0	3	11	0.86	1	700	927
36	0	74.4	15	1.47	7.6	1	1	0.57	1	624	1289
37	0	42	4	1.09	28.3	0	29	0.58	216	1	2603
38	0	59	2	0.71	40.0	0	52	0.50	200	1	2274
39	0	53	4	0.55	49.2	0	44	0.55	180	1	2511
40	0	59	18	0.69	30.5	0	0	0.69	80	1	2497
41	0	65	5	0.84	55.6	0	56	2.60	1000	1	4273
42	0	50	8	1.13	8.0	2	2	3.90	1	3000	5272
43	0	30	29	1.57	7.0	3	16	5.50	1	1	4707
44	0	96	4	1.17	60.2	0	45	2.34	125	300	6066
45	0	57	17	1.57	14.0	4	8	3.90	1	1	4746
46	0	87	3	0.91	45.2	0	63	1.00	120	480	3011
47	0	87	16	1.67	30.5	60	5	1.73	1	1	2026
48	0	72	22	2.07	20.0	15	15	0.50	72	120	3498
49	0	76	12	1.43	40.8	0	50	0.88	48	1920	4244
50	0	73	28	1.46	16.5	20	10	1.44	72	1	4749
51	0	47	81	1.64	19.3	1	6	3.00	1	100	3442
52	1	61	23	2.04	26.0	13	13	4.45	1	1	765
53	2	70	14	1.78	15.5	0	26	19.5	375	750	1772
54	1	55	30	1.16	15.0	0	30	43.7	96	1	1250
55	1	44	34	1.38	12.5	1	6	27.6	1	1	1467
56	1	38	18	1.35	25.0	3	27	1.10	50	100	1507
57	2	63	28	1.91	19.5	5	45	1.00	400	1	1811
58	1	72	35	1.46	17.4	8	5	2.93	313	780	757
59	0	87	47	1.76	15.6	6	60	1.50	1	500	1542

APPENDIX C
MARSH RABBIT DENSITY ESTIMATES

Table C.1--Estimates of rabbit densities and numbers based on pellet counts in the Lower Keys. (Session 1 = March 1991, Session 2 = July 1991, Session 3 = November 1991, Session 4 = March 1992, Session 5 = July 1992, Session 6 = November 1992, Session 7 = March 1993, Session 8 = July 1992).

	Session 1		Session 2		Session 3		Session 4	
Site	Rab/ha	Total	Rab/ha	Total	Rab/ha	Total	Rab/ha	Total
1	2.02	3.05	1.03	1.08	0.61	0.64	3.59	3.77
2	0.22	0.27	1.01	1.23	0.18	0.22	1.32	1.61
3	0.08	0.13	0.28	0.45	0.00	0.00	0.07	0.11
4	1.86	5.43	1.4	4.23	0.74	2.14	1.83	5.34
5	0.00	0.00	0.01	0.02	0.15	0.37	0.66	1.61
6	0.67	1.85	2.23	6.13	0.00	0.00	0.05	0.14
7	0.74	2.87	0.60	2.33	0.53	2.07	2.16	8.40
8	7.63	29.66	6.21	24.16	3.44	13.39	2.85	11.10
9	1.49	7.22	0.62	3.03	0.58	2.83	2.75	13.34
10	3.97	9.01	2.70	6.13	2.28	5.17	2.24	5.08
11	4.65	24.09	2.54	13.16	0.38	1.97	0.77	4.00
12	0.74	1.71	1.91	4.45	3.01	7.02	3.87	9.01
13	8.99	30.58	4.37	14.86	2.28	7.74	1.58	5.36
14	0.31	1.83	0.85	4.96	2.02	11.80	0.56	3.26
15					1.81	2.08	0.13	0.14
16					5.64	3.89	2.24	1.55
17					2.53	2.63	0.17	0.18
26	0.20	0.31	0.14	0.22	0.41	0.63	0.35	0.54
28	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.18
29			0.00	0.00	0.00	0.00	0.05	0.13
30	1.20	0.94	0.37	0.29	1.27	0.99	0.20	0.16
31							1.14	1.14
32							0.25	1.00
33	5.20	163.80	3.90	122.85	4.05	127.58	0.50	15.75
34					0.25	0.58	1.37	3.15
41			0.00	0.00	0.00	0.00	0.00	0.00
42			0.00	0.00	0.00	0.00	0.00	0.00
43			0.00	0.00	0.00	0.00	0.00	0.00
44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
51	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
53	0.17	3.32	0.13	2.54	0.76	14.80	0.91	17.82
56			0.28	0.31	0.51	0.56	0.97	1.07
57			0.13	0.10	0.15	0.12	0.51	0.51
58	0.67	1.96	0.40	1.17	0.25	0.74	0.00	0.00
59			0.00	0.00	0.00	0.00	0.00	0.00

Table C.1--Continued.

Site	Session 5		Session 6		Session 7		Session 8	
	Rab/ha	Total	Rab/ha	Total	Rab/ha	Total	Rab/ha	Total
1	1.32	1.62	0.31	0.33	1.50	1.58	0.12	0.12
2	1.94	2.37	0.84	1.03	1.20	1.46	1.86	4.22
3	0.11	0.18	0.00	0.00	0.56	0.91	0.75	1.21
4	0.27	0.78	1.16	3.39	1.36	3.98	0.91	2.43
5	1.49	3.62	0.00	0.00	0.00	0.00	0.00	0.00
6	0.25	0.68	0.00	0.00	0.16	0.44	0.04	0.45
7	2.43	9.45	1.95	7.59	1.52	5.93	1.16	4.52
8	4.39	17.07	0.44	1.71	2.01	7.79	1.74	6.79
9	0.83	4.04	2.69	13.09	2.01	9.75	0.75	3.63
10	1.90	4.31	0.64	1.45	2.63	5.98	3.34	3.63
11	0.33	1.71	0.28	1.45	0.24	1.22	0.41	2.11
12	0.78	1.81	2.23	5.21	4.40	10.28	4.15	9.68
13	3.06	10.40	1.21	4.13	0.56	1.91	1.25	4.24
14	0.91	5.30	0.95	5.51	2.81	16.37	1.91	11.14
15	0.00	0.00	0.00	0.00	0.00	0.00	0.19	11.14
16	0.11	0.07	0.18	0.13	0.64	0.44	0.00	0.00
17	0.58	0.60	0.00	0.00	0.00	0.00	0.00	0.00
26	0.50	0.72	1.43	2.23	0.80	1.25	0.99	1.56
28	0.17	0.60	0.43	1.50	0.64	2.25	1.02	3.57
29	1.00	2.48	0.29	0.71	0.80	2.01	2.66	1.66
30	0.41	0.32	0.57	0.45	1.12	0.87	0.83	0.65
31	0.08	0.08	0.07	0.07	0.32	0.32	0.32	0.32
32	0.25	0.10	0.21	0.86	0.24	0.95	0.13	0.50
33	5.31	167.27	2.43	76.50	1.21	37.90	0.90	28.20
34	0.25	0.57	0.07	0.16	0.16	0.39	0.00	0.00
41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
42	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
51	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
53	1.65	32.24	0.21	4.18	0.40	7.80	0.41	7.90
56	1.24	1.36	0.00	0.00	0.00	0.00	0.00	0.00
57	0.60	0.60	0.49	0.49	0.96	0.96	0.83	0.83
58	0.00	0.00	0.00	0.00	0.08	0.23	0.13	0.37
59	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

APPENDIX D
MARSH RABBIT PATCH OCCUPANCY

Table D.1--Presence of adult and juvenile Lower Keys marsh rabbits (Sylvilagus palustris hefneri) during the last 6 sessions.

Site	code	Adult3	Juv.3	Adult4	Juv.4	Adult4	Juv.j5	Adult6	Juv.6	Adult7	Juv.7	Adult8	Juv.8
1	1	1	0	1	0	1	0	1	0	1	0	1	1
2	2	1	0	1	0	1	1	1	0	1	0	1	1
3	1	0	0	1	0	1	0	0	0	1	1	1	0
4	2	1	0	1	0	1	0	1	1	1	0	1	1
5	1	1	0	1	1	1	0	0	0	0	0	0	0
6	1	0	0	1	0	1	0	0	0	1	0	1	0
7	2	1	1	1	1	1	0	1	0	1	0	1	1
8	2	1	1	1	1	1	0	1	1	1	1	1	1
9	2	1	0	1	1	1	0	1	0	1	0	1	0
10	2	1	0	1	0	1	0	1	0	1	0	1	1
11	2	1	0	1	0	1	0	1	0	1	0	1	0
12	2	1	1	1	0	1	0	1	0	1	1	1	1
13	2	1	0	1	0	1	0	1	1	1	0	1	1
14	2	1	0	1	0	1	0	1	0	1	0	1	1
15	1	1	0	1	0	1	0	1	0	1	0	1	0
16	1	1	0	1	1	1	0	1	0	1	1	0	0
17	1	1	1	1	0	1	0	1	0	0	0	0	0
18	1	0	0	1	0	0	0	1	0	1	1	1	0
19	1	0	0	0	0	0	0	0	0	1	0	1	1
20	1	0	0	0	0	0	0	0	0	1	1	1	0
21	1	0	0	0	0	0	0	1	0	0	0	1	0
22	1	1	0	0	0	0	0	0	0	1	1	0	0
23	1	1	1	1	0	1	0	0	0	0	0	0	0
24	1	0	0	0	0	0	0	1	0	1	1	1	0
25	1	1	0	1	0	1	0	1	0	1	0	1	0
26	1	0	0	1	0	1	1	1	1	1	0	1	1
27	1	0	0	0	0	0	0	1	0	0	0	0	0
28	1	0	0	1	0	1	1	1	0	1	1	1	0
29	1	0	0	1	0	1	1	1	1	1	0	1	1
30	2	1	1	1	0	1	0	1	0	1	0	1	1

Table D.1--Continued.

Site	code	Adult3	Juv.3	Adult4	Juv.4	Adult4	Juv.j5	Adult6	Juv.6	Adult7	Juv.7	Adult8	Juv.8
31	2	1	0	1	0	1	0	1	0	1	0	1	1
32	2	1	0	1	0	1	0	1	0	1	0	1	0
33	2	1	1	1	1	1	1	1	0	1	1	1	1
34	0	1	0	0	0	0	0	0	0	0	0	0	0
35	1	0	0	0	0	0	0	0	0	0	0	1	0
36	0	0	0	0	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0	0	0	0	0	0	0
38	0	0	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0	0	0	0	0	0	0	0	0
40	0	0	0	0	0	0	0	0	0	0	0	0	0
41	0	0	0	0	0	0	0	0	0	0	0	0	0
42	0	0	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0	0	0	0	0	0	0	0	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0	0	0
51	0	0	0	0	0	0	0	0	0	0	0	0	0
52	1	0	0	0	0	0	0	0	0	0	0	1	0
53	2	1	1	1	1	1	0	1	0	1	1	1	0
54	1	1	0	1	1	1	0	0	0	0	0	0	0
55	1	1	0	1	0	0	0	0	0	0	0	0	0
56	1	1	0	1	1	1	0	0	0	0	0	0	0
57	2	1	1	1	1	1	0	1	1	1	0	1	1
58	1	1	0	0	0	0	0	0	0	1	0	1	1
59	0	0	0	0	0	0	0	0	0	0	0	0	0

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BIOGRAPHICAL SKETCH

Elizabeth A. Forys was born September 12, 1966, in Berkeley, California. She attended the University of Virginia in Charlottesville, where she received a B.A. in environmental sciences and biology, in 1988. In 1990, Elizabeth received her M.S. in environmental sciences with a concentration in ecology. Her thesis title was "The effect of immigration on the demographic and genetic composition of Oryzomys palustris on the Virginia Barrier Islands". In August of 1990, she entered the graduate program in the Department of Wildlife and Range Sciences (currently the Department of Wildlife Ecology and Conservation) and will receive her Ph.D. in May of 1995. After graduation, Beth is returning to the Lower Keys to work on the recovery efforts of several endangered species.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Stephen R. Humphrey, Chairman
Professor of Forest Resources and Conservation

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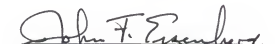

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